

蝶と蛾 *Tyô to Ga*, 40 (3): 197–228, 1989

Systematic Position of Libytheidae, Diphylgeny of Rhopalocera, and Heteroceran Ancestry of Rhopalocera (Lepidoptera)

Oakley SHIELDS

6506 Jerseydale Road, Mariposa, California 95338, U.S.A.

A reappraisal of the systematic position of Libytheidae, employing both adult and immature complex morphological characters that are largely external, indicates it evolved from a Pierinae ancestor and gave rise to Nymphalinae *sensu stricto*. The Libytheidae combine both pierid and nymphalid characteristics and is best regarded as a separate family. The results differ somewhat from those derived by cladistics which had missed its Pierinae derivation. An evolutionary series can be traced back from Pieridae through Lycaenidae to Lymantriidae. Rhopalocera probably arose diphyletically from Noctuoidea, viz. Lymantriidae-Lipteninae (Africa) and Agaristidae-Euschemoninae (Queensland). The general development of Ditrysia is also traced. Stem genera (derived directly from ancestors) to various ditrysiian families, identified by non-cladistic clustering by symplesiomorphy, include *Psychidarbela*, *Pemphigostola*, *Ancarista*, *Apoprogon*, *Euschemon*, *Lamproptera*, *Larinopoda*, and *Libytheana*. The resultant evolution of Rhopaloceran families obeys Cope's Rule. Inferences drawn from plate tectonics and associated non-Lepidopteran fossils indicate that strategic origin times were the mid-Oxfordian (Agaristidae), Albian (Euschemoninae), and Cenomanian (Lycaenidae).

KEY WORDS: -cladistics-characters-symplesiomorphies-morphology-evolution-Noctuoidea.

Introduction

A brief review of cladistic principles, methods, strengths, and weaknesses is in order since these taxonomic issues have undergone much debate, modification, and testing in recent years in various publications.

Cladistics establishes clades (monophyletic groups) from multiple, derived and new characters (synapomorphies) and polarity (direction of evolutionary change, or transformation series) ascertained by outgroup comparison or by ontogeny (recapitulates characters inherited from the ancestors) to reconstruct branching sequences but excludes all primitive characters (symplesiomorphies) as irrelevant except in establishing polarity and synapomorphies since they do not define specific relationships within a monophyletic group and are more extensive than the group under study (SCHAEFFER, HECHT, & ELDREDGE, 1972; ROSEN, 1974; ENGELMANN & WILEY, 1977; ARNOLD, 1981; PATTERSON, 1980, 1982a). The outgroup is a closely related group, preferably the closest relative to the group under consideration (ingroup), that is cladistically more basal. Similarities (symplesiomorphies) between the outgroup and ingroup are due to having a common ancestor that possessed the primitive condition of both. Ingroups and outgroups are relative terms, functioning at different levels depending on the characters studied (WATROUS & WHEELER, 1981).

Ideally all taxa within a cladistic classification are clades (BREMER, 1985), and cladograms are schemes of distribution of uniquely derived characters (SAETHER, 1986). Apomorphies are derived from plesiomorphies, and successive stages in a transformation series become more apomorphic (BOCK, 1977). Unshared derived characters (autapomorphies) confined to a single taxon cannot indicate relationships (ARNOLD, 1981). The method of arranging derived characters in tabular form for each taxon and constructing a cladogram from the shared characters is depicted by PATTERSON (1980, Table 2 & Figure 3). Synapomorphies are inherited in a modified form from the ancestor, while symplesiomorphies are inherited unchanged from the ancestor (WHEELER, 1986). Cladistics cannot include the common ancestor in the same monophyletic grouping as all of its descendants because of strict adherence to the criterion of synapomorphy. Since ancestral species are equivalent to the totality of all their descendant species, they are best placed in a distinct monotypic genus just before their descendants in phylogenetic relationship (WILEY, 1979).

But shared primitive characters (symplesiomorphies) must also be used to determine which groups were ancestral when constructing evolutionary phylogenies since evolution is concerned with both sister-group and ancestor-descendant relationships; derived characters are precisely those *not* present in the ancestor. Sister groups are each other's closest relatives (PATTERSON, 1982b). Symplesiomorphies do become synapomorphies of groups at a higher level (MICKEVICH, 1978). Synapomorphies and symplesiomorphies are relative terms that are defined in relation to the particular taxonomic level under consideration. Depending on which suite of derived characters chosen and their polarity criteria, different phylogenies can emerge (Le QUESNE, 1974; STEVENS, 1980; CRANE, 1985) even though only one true phylogeny is possible. A cladogram will err if the taxonomy it is based upon is faulty, such as species arbitrarily lumped, split, or placed in improper genera (WAGNER, 1980).

The need for character weighting of morphoclines (morphological transformation series) in cladistics is stressed by HECHT & EDWARDS (1976a,b) and SOBER (1986). Only *a priori* character weighting performed independently of cladistic analysis is valid, as *a posteriori* weighting involves circular reasoning and is performed from criteria dependent on the evolutionary systematic, phenetic, or sometimes cladistic analysis (NEFF, 1986). Character loss does not indicate evolutionary direction or relationships (HECHT & EDWARDS, 1976b), and character simplification is another problem. Fissioning of a functional complex of characters into many separate characters is undue weighting (HECHT & EDWARDS, 1976b). Constant, complex, consistent, and correlated characters deserve greater weight than do variable, narrowly specialized, or lost characters (WHEELER, 1986). Character weighting can decide between conflicting morphoclines, while sheer quantity of unweighted characters can actually prevent recognition of the real lineage (HECHT & EDWARDS, 1976a; ARNOLD, 1981; BREMER, 1985) although useful in recognizing parallel, convergent, and reversal evolution. Cladograms are rarely tested against the fossil record, a means of evaluating their conclusions with facts, particularly when it comes to which characters should be weighted over others (SZALAY, 1982; BROWN & ROSE, 1987). No weighting is necessary

only when determining the phylogeny of a complete or nearly complete fossil record (CAIN & HARRISON, 1960).

For five phenetic and three numerical cladistic methods tested for congruence between morphological and allelic data in eight different animal groups, only undirected and rooted trees consistently showed the greatest stability (MICKEVICH, 1978, 1980). WAGNER's method is based on essentially the same principles as HENNIG's cladistics (WILEY, 1981, p.178).

Cladistics often rejects relative degrees of similarity and its methodology ignores ancestors (living and fossil), except when determining polarity in its quest for shared unique (derived) characters (Van VALEN, 1978; JOHNSON and QUINTER, 1982), thus bypassing a significant part of evolutionary theory. Indeed, pattern cladistics is at odds with evolutionary theory (BOCK, 1968; SZALAY, 1977; ASHLOCK, 1979; BEATTY, 1982). In its misuse of parsimony to reflect true phylogenetic relationships and in its assertion that common ancestors are only hypothetical and cannot be recognized, cladistics can give an incomplete and misleading view of evolutionary history (SZALAY, 1977; PANCHEN, 1982; JOHNSON & QUINTER, 1982) even though it otherwise applies Darwinian evolutionary principles to classification. Parsimony cannot test hypotheses or their internal consistency; hypotheses are tested against empirical observations for validity and internal consistency is what theories must have before they can be tested (BOCK, 1977). The best theories explain as many and as wide a range of phenomena as possible and are not the most parsimonious. Popperian parsimony gives a sequence for testing hypotheses but is not itself a test, being merely a description of the content of an hypothesis (JOHNSON, 1982). When parsimony was tested against molecular changes in a known pathway of amino acid and nucleic acid sequences, it erred significantly (HOLMQUIST, 1979). The frequency of evolutionary reversals and opportunism insures that parsimony cannot reflect actual phylogeny (MAYR, 1981). Depending upon which outgroup is chosen, different plesiomorphic estimates can result (ROURKE, 1986). Plesiomorphies can reappear as mistaken apomorphies by evolutionary reversal in some instances. Much the same criticisms apply to the phenetic analyses of butterfly phylogeny of EHRLICH (1958a) and EHRLICH & EHRLICH (1967). In phenetics, characters are usually weighted equally and phylogeny is irrelevant to the classification (JOHNSON & QUINTER, 1982). Phenetics groups on overall similarity whereas cladistics groups only on synapomorphy. Cladistic methods have a much higher stability than do phenetic methods (MICKEVICH, 1978, 1980). To determine phylogenetic relationships, a few well-chosen complex characters sorted as to primitive, derivative, or convergent seem preferable to purely derived, unweighted characters which are more likely to undergo loss or change and to yield multiple phylogenies depending upon which characters are selected. Functional morphology can suggest initial interpretations of polarity and can help to resolve cases of incongruent apparent synapomorphies (FISHER, 1981). Cladistics usually disregards the functional and adaptational role of features during character analysis (SZALAY, 1982).

Methods

Recently two papers using cladistics have generated slightly different systematic positions for Libytheidae (KRISTENSEN, 1976; SCOTT, 1984). KRISTENSEN lumped Libytheidae with Nymphalidae *sensu lato* based on four synapomorphies (male foreleg, pupa free, antennal grooves, and a muscle character), while SCOTT concluded from a greater number of characters that Libytheidae could either be incorporated with Nymphalidae or retained as a separate family.

To overcome the shortcomings of cladistic methods in determining the systematic position of Libytheidae, another method was employed but is not meant as a challenge to cladistics. This consists of selecting complex morphological characters (Le QUESNE, 1974) in libytheid adults (as well as egg, larva, and pupa as ontogeny) and noting the preponderance of the similarities (affinities) of these characters in other butterfly families to determine libytheid's nearest relatives. As such it is concerned with reconstructing ancestors (i.e. stem groups connecting families) or at least the probable characters of the ancestors, unlike cladistics (except during morphocline analysis), and thus is a separate approach from cladistics (cf. HECHT, 1976; HEADS, 1985); it makes intimate use of symplesiomorphies in determining preservation of primitiveness (stasigenesis). It differs from phenetics which unites by both symplesiomorphies and synapomorphies (MICKEVICH, 1978). No attempt is made here to comparatively weigh complex characters except in assuming they carry greater weight than do simple characters. Paraphyletic groups are characterized by shared primitive characters (PATTERSON, 1982b), such as links between families.

Complex characters are unlikely to have arisen more than once (HARPER, 1976). A complex character is actually composed of many simple morphological characters that are functionally highly integrated and coevolve due to directional selection, such as the amniote egg, vertebrate eye, and mammalian ear ossicles (HECHT, 1976; HECHT & EDWARDS, 1976a, b; STEVENS, 1980). A character complex (= complex of characters) is functional and allows characters to be pooled together and weighted; unique, complex characters have the least chance of resulting from convergence since they are due to specific selectional forces acting upon an ancestor to a set of taxa (SZALAY, 1981). Under Dollo's Law, complex characters evolve in exactly the same way only once and when lost are not regained, uniting groups sometimes by symplesiomorphy and other times by synapomorphy (GOULD, 1970; FARRIS, 1977). Complex characters can be either primitive or derived and will minimize the number of parallelisms and reversals (HARPER, 1976; HECHT & EDWARDS, 1976a; ARNOLD, 1981). Reversals usually involve relatively simple instead of complex characters (HECHT & EDWARDS, 1976a; HARPER, 1976). Each of the complex morphological characters chosen for the Libytheidae (see Table 2 and text) are functional units that can be further subdivided into two to many simple characters.

Ancestors are plesiomorphic for all characters relative to their descendant taxa (ENGELMAN & WILEY, 1977; CRANE, 1985). Of course, ancestors can be verified only in groups with a good fossil record (WILEY, 1981), whereas the Rhopaloceran fossil record is relatively poor (SHIELDS, 1976; DURDEN & ROSE, 1978; JARZEMBOWSKI, 1980; LEEST-

MANS, 1983), confined to the Cenozoic, and is not useful in confirming the direction of evolutionary trends since few morphological characters are preserved. In phylogenesis, descendant species ultimately evolved from only one ancestral species and not from a supra-specific taxon (AX, 1984), though usually in practice the ancestor can only be determined at the generic, tribal, or subfamily level. Good characters are more conservative or nonadaptive and deserve greater weight in determining phyletic affinity than less conservative ones (WHIFFIN & BIERNER, 1972; SOBER, 1986). Characters are conservative if they show relatively little variation and are irreversible (STEVENS, 1980). Characters used in Wagner trees in general are conservative and are not assumed *a priori* to be either primitive or advanced (WHIFFIN & BIERNER, 1972).

Using the ontogeny recapitulates phylogeny approach (cf. WILEY, 1981, pp.153–158; de QUEIROZ, 1985) and the evolutionary ranking of their larval foodplants proposed by botanists (Table 1) as guides, the morphological characters were sorted (polarized) as to primitive (symplesiomorphies) and intermediate and derived (synapomorphies). Ontogeny is useful because of ancestral character retention and elimination of derived characters (de QUEIROZ, 1985); outgroup comparison introduces unwanted variability depending upon which outgroup is used for comparison, unless the closest relative of the whole group under consideration is known and used. This method insures that relative degrees of symplesiomorphic similarity and ancestors are taken into account. *The value of morphotypes (multiple morphological characters presumably present in the ancestor) lies in greatly reducing the range of morphology within which the ancestor may be sought* (MAYR, 1974; SZALAY, 1977). The method is to scan the total variation, seeking points of *greatest* morphological resemblances (HECHT, 1976), and is a form of outgroup comparison, i.e. closely related taxa that presumably share the same ancestry and thus the same ancestral characters. “The higher the number of primitive character states held in common by a group of organisms, the closer we may come to defining a hypothetical common ancestor” (SCHAEFFER, HECHT, & ELREDGE, 1972), estimated by clustering plesiomorphies (WAGNER, 1980). Closely related groups will share a larger number of common characters than will more distantly related groups (HARPER, 1976). Primitive characters are the oldest ones evolutionarily and can be determined by oldest fossils, commonly distributed characters, out-group comparison, and ontogeny (CRISCI & STUESSY, 1980). Character states most widely distributed among the taxa are considered to be the most primitive or ancestral (EYDE, 1971; HECHT & EDWARDS, 1976a; ESTABROOK, 1977; de QUEIROZ, 1985), and a primitive taxon retains a large number of primitive characters relative to some other taxon (HEYWOOD, 1977). The ancestor possesses all the plesiomorphic states from which the descendants have diverged (WAGNER, 1980). In cladistics, character states that the in-group, sister-group, and out-group have in common are considered ancestral (ROURKE, 1986). Outgroup comparison identifies plesiomorphies that are present in both the group under consideration and its nearest relatives (BROOKS & WILEY, 1985).

A literature search uncovered some other Lepidopteran genera that are transitional between families and thus indicate evolutionary directions. Phenotypic similarities in adult Rhopalocera, however, were not always useful because of widespread

mimicry. Müllerian mimicry can arise by either convergent or parallel evolution and Batesian mimicry by advergent evolution (BROWER & BROWER, 1972), producing a false sense of phyletic closeness. Non-mimetic parallel and convergent evolution occurs frequently within Pierini (SHAPIRO, 1979).

The method used here emphasizes shared primitive (generalized) characters in ancestor determination, while cladistics emphasizes the shared derived (advanced or specialized) state of descendants. Relatively speaking the former looks backward and the latter looks forward at evolutionary progression by emphasizing symplesiomorphies and synapomorphies, respectively (SOBER, 1986). Combining the ancestor stem-group (symplesiomorphies) method with the cladistic descendant-branching (synapomorphies) method should produce a classification that is entire and congruent with phylogeny (phylogenetic classification) (see SZALAY, 1977). Without a good fossil record as an independent test of cladistic prediction, a morphocline can never be proven or falsified with certainty, although far fewer possible phylogenies are generated by this ancestor method than by cladistics. The basic assumption is that "all character states found in the oldest fossils of a group are the most primitive" for groups with a good fossil record (CRISCI & STUESSY, 1980). That an ancestral character is usually associated with other ancestral characters is indeed substantiated by the fossil record in angiosperms for pollen, woodiness, and floral characters, with the derived characters for these conditions appearing later in time (EYDE, 1971). The cladogram is also congruent with the fossil record in Balfourianae pines (ROURKE, 1986). Morphocline polarity can be determined by relative stratigraphic position of fossils in combination with cladistics of living forms to yield an empirical reading of phylogeny; when the fossil record is dense and continuous, a clear pattern emerges, but when large gaps exist (as in Rhopalocera), the pattern is ambiguous but still suggestive (GINGERICH, 1979). Fossils can give the actual course of character transformation through time (ELDREDGE & NOVACEK, 1985). Cladograms can be used to reveal inconsistencies with taxonomic rates indicated by insufficient fossil data if the fossil record fails to corroborate the cladogram (NOVACEK & NORELL, 1982).

Ancestral groups (e.g. in Orthoptera) often persist for considerable lengths of time after their descendant groups originated from them in geographically or ecologically isolated populations, instead of quickly becoming extinct by direct competition with the new groups (SHAROV, 1965). Thus the idea that no modern taxon can be ancestral to another modern taxon is not always true. "Living fossils" (bradytely, arrested evolution) include *Lingula*, bairdiid ostracods, nuculoid bivalves, monoplacophoran molluscs, oysters, *Peripatus*, *Limulus*, lungfish, *Latimeria*, gars, turtles, crocodilians, *Leiopelma*, *Sphenodon*, ratites, *Ginkgo*, and others. These groups have a predominance of symplesiomorphies and often have relict distributions (ELDREDGE & STANLEY, 1984). The fossil record indicates that speciation events produce rapid change while the subsequent gradual evolution of established species is comparatively minor (STANLEY, 1975). At the other end of the evolutionary spectrum is macroevolutionary change—the sudden appearance and subsequent specialization of distinctive new features and taxa (such as families). Macroevo-lutionary change involves the punctuated

equilibria model of allopatric speciation in small isolated or founder populations under new environments (BOCK, 1979; VRBA, 1980; MAYR, 1982). Such populations have a small fraction of the total genetic variability, possess little or no gene flow, are under increased environmental selection pressures producing very rapid evolutionary rates, and may shift to new niches under changed environments due to morphological innovations (BOCK, 1979; MAYR, 1982). Macroevolutionary changes most often occur at geologic time boundaries following extinctions and are followed by a period of comparatively rapid radiation (explosive evolution) into a number of adaptive zones.

Results

Immatures

The eggs of libytheids are somewhat bottle-shaped, about twice as high as broad, forming a short neck or stalk close to the apex, with strong vertical, elevated ribs; between the ribs are numerous horizontal, minute, raised cross-lines (SCUDDER, 1889a; WATERHOUSE & LYELL, 1914; COMMON & WATERHOUSE, 1972). References to descriptions of various species of libytheid eggs are given in SHIELDS (1985a). The eggs vary in shape, number of ribs, and numbers of cross-lines. Some authors have noted a close resemblance of libytheid eggs to pierid eggs such as *Mylothris* (e.g. BELL, 1910; WYNTER-BLYTH, 1957; CLARK & DICKSON, 1964; CORBET & PENDLEBURY, 1978). Others point out that in *Libytheana* the vertical ribs that terminate abruptly at the rim of the flattened summit recall *Polygonia* (EDWARDS, 1884; SCUDDER, 1889a), or in *Libythea celtis* FUESSLY some of the vertical ribs continue as high flanges as in Nymphalinae (CHAPMAN, 1912). BROWN and HEINEMAN (1972) conclude that libytheid eggs are intermediate in shape between pierids and nymphalids and are vertically ribbed as frequently occurs in both of these families.

In general the larva of *Libytheana bachmanii* KIRTLAND resembles those of the Pieridae and not Nymphalidae (see PETERSON, 1962). The head is small and covered with secondary setae. Each abdominal segment is divided into 4 or 5 annulets. They lack scoli that are present on the head and/or body of Nymphalidae. *Libythea celtis* is like Pieridae larvae in having a cylindrical body with numerous secondary setae, also on the head, and is distinguished from them only by the presence of the lateral rudimentary crochets of the pseudocircle (FRACKER, 1915). Many other authors have remarked on the strong resemblance of libytheid larvae to those of the Pieridae (e.g. TRIMEN, 1887; NICÉVILLE, 1900; WATERHOUSE & LYELL, 1914).

Potential pierid ancestors to libytheids to be discussed shortly utilize mistletoes as larval foodplants: *Melete* uses *Phoradendron* (Loranthaceae) and *Mylothris* uses *Loranthus* and *Viscum* (Loranthaceae) and *Osyris* (Santalaceae). Structurally *Melete* and *Mylothris* are closely related (KLOTS, 1931). *Melete* (13 species) occurs in the tropics of Mexico, Central and South America, Cuba, and Hispaniola, while *Mylothris* (43 species) is confined to the Ethiopian and Malagasy regions (TALBOT, 1932). Perhaps the first libytheids evolved from *Melete* or *Mylothris*-like pierids that switched from mistletoe to *Celtis* (Ulmaceae) as larval foodplants; e.g. in Japan, *Viscum* parasitizes *Celtis sinensis* PERS. (SAKURAI & OKUMURA, 1971). Food-plants are in the category of

ecological characters (WILEY, 1981).

The pupa of *Libytheana* is suspended by the cremaster and lacks a silken girdle as in nymphalids and unlike pierids (EDWARDS, 1884; SCHREITER, 1943; COMSTOCK & GARCIA, 1960). The nymphalid pupa is essentially a pierid pupa that has lost the girdle (CHAPMAN, 1895). Only the more advanced families of butterflies have pupae that hang freely by cremastral attachment only (MILLER, pers. comm.). The cremastral surface of *Libythea celtis* is narrow and straight in an antero-posterior line as in Nymphalinae (CHAPMAN, 1900b). The cremastral hooks of *Libythea laius* TRIMEN pupae are like nymphalids and unlike pierids (cf. RILEY, 1880; CLARK & DICKSON, 1964). The pupa of libytheids resembles overall a nymphalid pupa (e.g. *Ergolis*, *Pseudergolis*, or even *Pararge*, *Eurytela*, *Neptis*) and has no more pierid characteristics than any other nymphalid has (CHAPMAN, 1900b; BELL, 1910; WYNTER-BLYTH, 1957; CLARK & DICKSON, 1964). However, the pupal form of libytheids is also similar to certain *Pieris* species (see COMSTOCK, 1927).

Wings

Libytheid wing venation (cf. SCUDDER, 1889b; PAGENSTECHER, 1901; BATES, 1935; COMSTOCK, 1944; AOKI, YAMAGUCHI & UEMURA, 1982) is extremely similar or even identical with certain Pieridae and Nymphalidae (GROTE, 1898; 1900).

The wings of *Libytheana bachmanii larvata* STRECKER contain the pterin pigments xanthopterin, isoxanthopterin, erythropterin, and leucopterin, and some of these same pigments are present in other libytheids although are lacking in a few Old World species (SHIELDS, 1987). Pieridae is the only other family of Rhopalocera known to contain all these wing pigments. Pterins are known to occur in the wings of one *Heliconius* (erythropterin) and occasionally in some Nymphalidae, Lycaenidae, Riodinidae, and Papilionidae (isoxanthopterin) but never in the array present in pierids and libytheids. Pterins are an example of a physiological character (WILEY, 1981). The wing shape of libytheids is similar to certain Nymphalinae such as *Polygonia* and is convergent with certain African *Epitola* (Epitolinae).

Forelegs

In Libytheidae the male forelegs are aborted and rudimentary, slender, greatly reduced in size (one-quarter the other legs), brush-like tibia and tarsus, densely hairy, with the single-segmented tarsus shorter than the tibia and lacking claws or spines (TRIMEN, 1887; LEECH, 1893; FIELD, 1938; COMMON & WATERHOUSE, 1972; DICKSON & KROON, 1978). In *Libythea celtis* the male foreleg is usually completely hidden among body hair and may appear missing (KAWAZOÉ & WAKABAYASHI, 1976).

The female scaly forelegs, though slightly reduced in size and slender compared with the other legs, are fully developed and functional (SCUDDER, 1889a; EHRLICH, 1958a; DICKSON & KROON, 1978). The female tarsus is five-segmented with minute but normal falciform claws, bifid and slender paronychialia, and a pair of bifid pulvilli (TRIMEN, 1887; SCUDDER, 1889a; LEECH, 1893; COMMON & WATERHOUSE, 1972; KAWAZOÉ & WAKABAYASHI, 1976). The tarsus is armed with short spines beneath (LEECH, 1893).

Thus the foreleg structure of Libytheidae is like the Nymphalidae in the male but differs from all Nymphalidae in the female excepting *Pseudergolis* (JORDAN, 1898).

Like the Pieridae, the foreleg of Libytheidae females has two bifid claws and also agrees with them in having paronychial and pulvilli (HOLLAND, 1955; EHRLICH & EHRLICH, 1961; COMMON & WATERHOUSE, 1972; HIGGINS, 1975; DICKSON & KROON, 1978; CORBET & PENDLEBURY, 1978; SCOTT, 1986a). In Nymphalidae females the foreleg tarsus often has less than 5 segments and lacks tarsal claws except in a few Ithomiinae and Calinaginae (COMMON & WATERHOUSE, 1972; SCOTT, 1986a) although the nymphalid foretarsus is armed with strong spines as in libytheids (HIGGINS, 1975).

Male genitalia

The sum of the main genitalia characters of *Libythea celtis* places it both with Pieridae and Nymphalidae (WHITE, 1878). Comparing the genitalia drawings of *Libythea* and *Libytheana* (SHIELDS, 1985a) with pierid genera (KLOTS, 1930, 1931), only *Melete*, *Mylothris*, and *Euchloina* are similar (but not identical) in whole aspect of valve, aedeagus, and the uncus-tegumen-vinculum-saccus. The arm-like process of the tegumen in *Libytheana* is homologous to the appendix angularis commonly present in Nymphalidae (KAWAZOE & WAKABAYASHI, 1976). *Libythea* resembles Nymphalidae in the presence of a long aedeagus, aspect of the saccus, and valve with projecting processes and hooks (SCUDDER, 1889a; MEHTA, 1933). The valve and well-developed, chitinous uncus of *Libythea* compare closely with that of Nymphalidae (FRUHSTORFER, 1914).

Labial palpi

Traditionally the libytheids are distinguished from nymphalids with which they agree in venation by the long, porrect, beak-like labial palpi in all species and the female forelegs (COMMON & WATERHOUSE, 1972). They also differ from nymphalids in possessing a median apical process on the eighth abdominal tergite in the males (FRIEDLANDER, 1984; FRIEDLANDER, pers. comm.). A detailed study of the libytheid labial palpi compared with other butterflies is given by REUTER (1896). Labial palpi of comparable appearance and shape to libytheids occur in *Cyblisia*, *Libythina*, *Vanessa*, and *Rhinopalpa* (JORDAN, 1925).

In repose libytheids on twigs rest tipped forward with their wings closed, the forewings and abdomen tucked inside the hindwings, thus simulating an old, dried, or dead leaf in underside coloration with the median vein strongly darkened like the leaf mid-rib and the antennae and palpi tightly pressed together and touching the twig or branch, perfectly simulating an attached leaf; they are unique in butterflies in assuming this pose (KUSNEZOW, 1900). This is an example of a behavioral character (WILEY, 1981). The elongated labial palpi probably evolved to perfect the leaflike camouflage (SCOTT, 1986a). No living pierids have palpi as long as in libytheids although the *Melete* palpus has a slender third joint, much longer than the second (KLOTS, 1931) as in *Libythea*, and the Lower Oligocene Florissant Pierinae (Pierini) fossil, *Stolopsyche libytheoides* SCUDDER, has a long palpus (SCUDDER, 1889b).

Antennae

The Nymphalidae antenna always has two grooves on the ventral surface that are diagnostic and distinguish them from other butterfly families, while Pieridae have a single groove as a row of separate or merging large pits (JORDAN, 1898; CHAPMAN,

1900a). *Libytheana* and *Libythea* clearly have two ventral grooves on the antenna (JORDAN, 1898; SHIELDS, 1985a), thus placing them with Nymphalidae instead of Pieridae in this regard. However, on the ventral surface of the antenna outside the grooves in both *Libytheana bachmanii* and *Colias* there is extensive ultrastructure pitting (SELLIER, 1974; SHIELDS, 1985a).

Eyes

Eye structure of *Libythea celtis* such as the pseudopupil form, scanty interfacial hair, and presence of iridescent iris pigments place it very near *Gonepteryx* (Pieridae) and *Melanitis* (Satyrinae), although the larval form of the latter is unlike libytheids (YAGI & KOYAMA, 1963; SIBATANI, 1973). In the rosette form of its reticular sense cell, Libytheidae stands between Pieridae and Satyrinae and not near Nymphalidae.

Discussion

Libytheidae and Nymphalidae

The mostly morphological characters for Libytheidae analyzed here are summarized in Table 2. The ova are both close to pierids and intermediate between pierids and nymphalids, the larva is close to Pieridae and not Nymphalidae, and the pupa is closest overall to Nymphalidae. Thus the immatures show a transformation series. The adult libytheid combines both Pieridae and Nymphalidae characteristics; the primitive characters of pterin pigments and eyes side with Pieridae; the intermediate characters of wing venation, forelegs, and male genitalia resemble Pieridae and Nymphalidae equally; while the derivative characters of the specialized labial palpi and the antennae side mostly with Nymphalidae. Once primitive and derived states have been deciphered, one can then reconstruct a hypothetical polarity (HECHT & EDWARDS, 1976a). The characters, when combined with the principle of ontogeny recapitulates phylogeny, the trend in larval foodplants in Table 1, and silken girdle loss, strongly suggest that the evolutionary direction was from a Pierinae ancestor through Libytheidae to Nymphalinae *sensu stricto* and not the reverse. Superficially Libytheidae recall the Riodinidae in the forelegs but widely differ from them in appearance, head, venation, immatures, palpi, genitalia, biserrate antennae, chaetosema organ, etc. (SCUDDER, 1889a; GODMAN & SALVIN, 1879–1901; AURIVILLIUS, 1919; JORDAN, 1925; FORBES, 1960; WYNTER-BLYTH, 1957; BROWN & HEINEMAN, 1972). Some Pronophilini Satyrinae approach libytheids in palpi length, wing pattern, and forewing shape, but they drastically differ from them in feeding on monocots, egg structure, larvae with bifid tails, greatly reduced female forelegs, male genitalia, and chromosome numbers (FORSTER, 1964; de LESSE, 1967; MILLER, 1968; L. MILLER, pers. comm.). Libytheidae share very few characters at all with Hesperidae, Papilionidae, and Lycaenidae.

The higher systematics of the large and diverse family Nymphalidae are variously treated without a consensus being reached (cf. REUTER, 1896; CLARK, 1947, 1948; ORFILA, 1949, 1950; EHRLICH, 1958a; EHRLICH & EHRLICH, 1967; ACKERY, 1984; De VRIES, KITCHING & VANE-WRIGHT, 1985). The data herein suggest that Nymphalinae *sens. str.* arose from a Pierinae ancestor via the Libytheidae.

A tympanic organ is present at the wing base in various Nymphalidae (absent in

Table 1. Amentiferae larval foodplants of Libytheidae and Nymphalinae close relatives. The classification of Amentiferae families follows MEARS (1973) and BERG (1977). *Libythea celtis* also uses *Paliurus* (Rhamnaceae) (DEGTYAREVA, 1961), and *Nymphalis californica* BOISDUVAL uses various species of *Ceanothus* (Rhamnaceae). Rhamnaceae is sometimes placed adjacent to and following Urticales in relationship (e.g. THORNE, 1973).

Libytheidae

Libytheana—*Celtis* (Ulmaceae)

Libythea—*Celtis* (Ulmaceae), *Prunus* (Rosaceae)

Nymphalinae

Hypanartia—*Celtis*, *Trema* (Ulmaceae), *Boehmeria* (Urticaceae)

Polygonia—*Celtis*, *Ulmus* (Ulmaceae), *Boehmeria*, *Urtica* (Urticaceae), *Humulus* (Cannabaceae), *Betula*, *Alnus* (Betulaceae), *Salix*, *Populus* (Salicaceae), *Prunus* (Rosaceae), *Ribes* (Grossulariaceae)

Nymphalis—*Celtis*, *Ulmus* (Ulmaceae), *Urtica*, *Laportea* (Urticaceae), *Humulus* (Cannabaceae), *Betula* (Betulaceae), *Salix*, *Populus*, *Toisusu* (Salicaceae), *Prunus* (Rosaceae)

Vanessa—*Celtis*, *Ulmus* (Ulmaceae), *Boehmeria*, *Laportea*, *Urtica*, *Girardinia*, *Parietaria* (Urticaceae), *Humulus* (Cannabaceae)

Table 2. A comparison of complex characters of Libytheidae with Pieridae and Nymphalidae.

OVA—some as in Pierinae, others intermediate between Pierinae and Nymphalinae.

LARVAE—close to Pieridae (not Nymphalidae).

PUPAE—like Nymphalidae and a few Pierinae in form but only Nymphalidae in cremastral hooks and suspension.

ADULTS

Wings—pterin array in *Libytheana* and Pieridae (not Nymphalidae); venation as in certain Pieridae and Nymphalidae.

Forelegs—like Pieridae in female structure but with tarsal spines as in Nymphalidae; like Nymphalidae in males (not Pieridae).

Male Genitalia—like certain Pierinae and Nymphalidae.

Labial Palpi—long like a few Nymphalidae (also one fossil Pierinae).

Antennae—like Nymphalidae (not Pieridae) in two ventral grooves; *Libytheana* like some pierids in ventral ultrastructure pitting.

Eyes—like certain Pieridae and Satyrinae (not other Nymphalidae).

Libytheidae, Nymphalinae, and other butterflies) in certain Brassolinae, *Morpho*, *Euptychia*, *Charaxes*, *Pseudergolis*, *Ergolis*, *Ageronia*, *Peridromia*, *Catagramma*, and *Heliconius* (Le CERF, 1926; SWIHART, 1967). The larvae of Brassolinae and Charaxiinae (especially *Charaxes*) are strikingly similar in cephalic horns and bifid tail (BATES, 1932). The larvae of *Calinaga* (Calinaginae, montane Southeast Asia) on *Morus* (Moraceae) possess twin spiny cephalic processes and a bifid tail characteristic of satyrines and morphines, with a somewhat egg-shaped, smooth pupa similar to *Morpho* and Danainae (EHRlich, 1958b; ASHIZAWA & MUROYA, 1967). The egg and antenna of *Calinaga* are most similar to *Danaus* (Danainae) (WATSON, 1899); Calinaginae and Danainae both have similar slow flight, wing pattern, coloration, and leathery, naked abdomens. Perhaps the specialized larval bifid tail subfamily series arose from Calinaginae. The only Danainae phenotypically similar to *Calinaga* is the advanced

genus *Parantica*. *Anetia* (Clothildini, montane southern Mexico to Panama, Cuba, Hispaniola) is cladistically the most primitive Danainae genus (ACKERY & VANE-WRIGHT, 1984) and likely evolved from Argynninae based on very similar wing pattern and larvae. Argynninae is considered a tribe of Nymphalidae *sens. str.* by some (e.g. ORFILA, 1950). The distinctive alimentary canals of nymphalines and satyrines are quite similar (HOMMA, 1954).

Pieridae

The ancestor of Pieridae has often been assigned to Papilionidae, but Pieridae larvae fundamentally differ from them in lacking the osmaterium universally present in Papilionidae (EHRlich & EHRlich, 1961), Papilionidae adults lack a horizontal chambered aorta present in all other butterfly families (HESSEL, 1966, 1969), the array of pterin pigments in the wings of Pieridae is lacking in Papilionidae (SHIELDS, 1987), and Papilionidae is not close to Pieridae by cladistics (KRISTENSEN, 1976). However, ant-tended larvae of many Lycaenidae and some Riodinidae (e.g. *Anatole*, *Hamearis*, *Theope*, *Nymphidium*) are also known in other butterflies only in the early instars of Pierinae such as certain *Leptidea*, *Pieris*, and *Anthocharis* which possess honey-glands on apically forked setae (HINTON, 1951). *Larinopoda* (11 species, primarily tropical West African in origin, especially Cameroon) is placed in the *Liptena* section of Lipteninae (the most primitive subfamily of Lycaenidae) by ELIOT (1973) but in male genitalia and facies is considered intermediate between *Eronia* (Pierini) and *Deloneura* (Lipteninae), the natural position in Pierinae being between *Nepheronia* and *Euchloe* (BUTLER, 1871; ELTRINGHAM, 1922; STEMPFFER, 1967). However, Celastrales-feeding *Eronia* and *Nepheronia* are much larger than *Larinopoda* in size. Structurally *Eronia* and *Nepheronia* are quite closely related (DIXEY, 1910; KLOTS, 1931), and *Eronia* and *Euchloe* are very similar in facies and pupae (DIXEY, 1894). Thus *Larinopoda* may well be closer to the ancestor of Pieridae than is Papilionidae. They are small and white or cream-colored with shaded or black distal markings. The Pieridae and Lycaenidae show other common characters in antennal grooves, endodont tarsal claws, and venation (CLENCH, 1955).

A closer relative to *Larinopoda* may be *Pseudopontia* which also has strongly rounded wings and ranges between the Sierra Leone and western Ugandan tropics (common in Cameroon). In the forewing of *Pseudopontia*, R_1 and R_2 are elbowed in an upward curve near their point of origin; anastomosis or contact of R_1 and R_2 also occurs in the *Epitola* section of Lipteninae and certain other lycaenids (GROTE, 1898; ELIOT, 1973). *Pseudopontia* ancestrally shows morphological relationships to both Pierinae and Dismorphiinae such as *Leptidea* (GROTE, 1900; KLOTS, 1931; KRISTENSEN, 1976). It is the only butterfly known with antennae tending to be clubless and distally bead-like.

Lycaenidae and Lymantriidae

The larvae of certain Lipteninae (e.g. *Hewitsonia*, *Iridopsis*, *Teratoneura*, *Epitola*, *Ebepius*) widely differ from other lycaenids and resemble the moth family Lymantriidae in form and coloration, with a broad and barely retractile head and dorsal and lateral hair tufts (BALDUF, 1939; STEMPFFER, 1967; ELIOT, 1973). *Terato-*

neura isabellae DUDGEON is the only butterfly known with urticating-type spicules, also present in certain Lymantriidae; it has two glands on the mid-dorsal line of segments 9 and 10, characteristic of lymantriids (BALDUF, 1939). A number of *Euproctis* (Lymantriidae) have "peppery" wings, also present in some Lipteninae. Some lymantriids and a few lycaenids have the unusual feature of specialized scales adhering to the eggs (ELIOT, 1973). Larval honey glands and tubercles characteristic of most Lycaenidae are lacking in Lipteninae (HENNING, 1983) and Lymantriidae. The lymantriid *Naroma signifera* WALK. is found in ant-runs where it feeds on a lichen (HINTON, 1951). Certain lymantriid-like Lipteninae are usually lichen-feeders (POULTON, 1917). The proboscis is reduced in *Durbania* (Lipteninae) and Lymantriidae. The chromosome numbers for Lipteninae (3 genera) and Lymantriidae (6 genera) are quite similar (ROBINSON, 1971). Some 82% of the larval foodplants for Lymantriidae are the same families used by lycaenids *sensu lato* (cf. BEESON, 1941; EHRLICH & RAVEN, 1965). The most lycaenid-like Lymantriidae are in the most primitive subfamily, Lymantriinae (BRYK, 1934). Africa is the center of species concentration in Lymantriidae (COLLENETTE, 1953), Lipteninae is confined to the Ethiopian region, and Africa has the main concentration of Lycaenidae subfamilies. Lymantriidae are generally nocturnal but a few are diurnal. The larvae of *Poritia* resemble Lymantriidae and Poritiinae larvae are gregarious and processionary like some Lymantriidae. The great and early success of Lycaenidae compared with Lymantriidae may be due to their symbiosis with ants, frenulum loss, functional proboscis, and clubbed antennae for diurnal activity. Since butterflies almost certainly arose from moths, the progression from Lymantriidae through Lycaenidae to Pieridae strongly indicates that Pieridae are more primitive than Nymphalinae; Libytheidae most likely is a transitional group between Pierinae and Nymphalinae in this sequence.

The geological time-frame for when the Lycaenidae-Libytheidae family series first originated can be inferred from fossils. The first primitive ants (*Sphecomyrma*, the extinct subfamily Sphecomyrminae of Russia) appeared during the Cenomanian-Turonian stages of the lower Upper Cretaceous (97.5 – 88.5 Myr ago) (WILSON, 1987; KENT & GRADSTEIN, 1985). The first extant *Celtis* appeared during the uppermost Cenomanian (93 – 91 Myr ago) in Borneo, when angiosperms increased in abundance and started diversifying there (MULLER, 1968, 1974). Angiosperms became dominant worldwide after the end of the Turonian, 88.5 Myr BP (RAVEN, 1977). The earliest libytheid fossils are two extinct species of *Libythea* from the Lower Oligocene of Colorado that are closely allied to two divergent existing species, indicating a long prior history (SHIELDS, 1985b). An advanced Noctuidae egg is known from the earliest Campanian (upper Upper Cretaceous) of Massachusetts (GALL & TIFFNEY, 1983). The few lycaenid, pierid, libytheid, and nymphalid generic and close genera links between the Ethiopian and Neotropical realms (SHIELDS & DVORAK, 1979) likely occurred before Africa and South America completely separated, during the lower Lower Turonian (Vascoceratan) 91 Myr ago (REYMENT, 1969; KENNEDY & COOPER, 1975).

Riodinidae

A number of features suggest the Riodinidae arose from the Lycaenidae (cf. ELIOT,

1973; SCOTT, 1984; ROBBINS, 1988). In Oriental Curetinae the male genitalia shows a close relationship with Oriental Abisarini Nemeobiinae in the distinctive uncus and valvae, and the foreleg coxa is produced slightly below its articulation with the trochanter, more pronounced in Riodinidae. Nemeobiinae is the most primitive subfamily of Riodinidae (STICHEL, 1930). Lipteninae and some Neotropical riodinids share certain common features in male genitalia, and sparse tufts of bristles on the ventral side of the abdominal segments of Poritiinae larvae also occur rarely in riodinids. Tubercles and honey glands used in ant symbiosis are found in many lycaenid larvae and a few riodinids like *Anatole* (ROSS, 1966), and stridulating pupae occur in Lymantriidae (and a few other moths), Lycaenidae, and Riodinidae (HINTON, 1948; DOWNEY, 1966; DOWNEY & ALLYN, 1973). Riodinidae is a good-sized family with 123 genera and about 1300 species. Ridinidae differ from Lycaenidae in having smaller, non-functional forelegs with coxae extending spinelike below the trochanter articulation (slightly in Curetinae) in the male and hindwing with a vein along the base of the coastal margin (EHRlich, 1958a). Cladistically the Lycaenidae and Riodinidae are separate families (ROBBINS, 1988).

Hesperiidae

By cladistic analysis, Hesperiidae is the most primitive Rhopaloceran family, followed by Papilionidae (KRISTENSEN, 1976). The monotypic *Euschemon* (Euschemoninae) from the coastal jungles of northeastern Queensland and northern New South Wales has similar venation, long curved antennae, markings, and coloration to Agaristidae (e.g. *Scrobiger*) and possesses a well-developed frenulum and retinaculum in the male, otherwise unknown in Rhopalocera but present in many higher Ditrysia including Agaristidae. Both Agaristidae and Hesperiidae lack pigment in the clear zone of the eye (SCOTT, 1986b), and anthoxanthins are especially common in both families (FORD, 1941). Northeastern Queensland also has the highest concentration of relict genera of dicot angiosperms (MELVILLE, 1975). *Euschemon* larvae feed on Monimiaceae, a very primitive family of Laurales. Loss of the frenulum and retinaculum in the *Euschemon* female and subsequently in all other Hesperiidae, together with the development of the amplexiform type of wing-coupling, allowed a greater amplitude in the wing-stroke (TILLYARD, 1918). Euschemoninae is closely related to Pyrginae which often have a unique coastal fold in the males, possibly a specialization of the agaristid sound-box, that later became the male forewing stigma of Trapezitinae and Hesperinae. *Euschemon* is placed next to *Chaetocneme* (Pyrginae) of coastal eastern Australia, New Guinea, and the Bismarck Archipelago by early stages and structure (EVANS, 1949). MEYRICK (1902), TILLYARD (1919), VOSS (1952), and TINDALE (pers. comm.) regard *Euschemon* as the hesperiid prototype. Pyrginae has two tribes, Pyrgini and Urbanini (ORFILA, 1949). In early-formed pupae, Hesperiidae retain the greatest number of primitive venation characters of Rhopalocera (TINDALE, 1980), and in having a large head and antennae spaced far apart, they are moth-like (RAINBOW, 1907). The compound eye of Hesperiidae is transitional in form between Rhopalocera and Heterocera, having features in common to both (MILLER, BERNARD & ALLEN, 1968). The well-defined subfamily Megathyminae has venation like Hesper-

iinae (EVANS, 1955).

Papilionidae

Papilionidae likely arose from very primitive Pyrginae (e.g. the *Urbanus* group) on the basis of smooth green larvae, Laurales food-plants, pupal suspension, and general adult morphology (MUNROE, 1949). Ranales foodplants for Pyrginae include Lauraceae, Annonaceae, and Piperaceae. The only papilionid that resembles Pyrginae in small size and appearance is *Lamproptera* (jungles of Southeast Asia, Indonesia, and Philippines). Within Graphiini, the most primitive genitalia occur in *Lamproptera* (MUNROE, 1949, 1960). It resembles a long-tailed Pyrginae in gross aspect, 3-segmented palpi, and tarsal claws bifid (other papilionids except *Graphium payeni* BOISDUVAL have simple tarsal claws). *Lamproptera* is a very distinct genus of Graphiini, especially in long, narrow tails, long antennae, veins 11 and 12 of the forewing free, and low swift flight (TALBOT, 1939). Cladistically the Graphiini is the most primitive tribe of the Papilioninae (MILLER, 1987). *Lamproptera* is distinct enough from Graphiini to justify a tribe of its own (CLARK, 1948). The larva has an osmaterium and feeds on Hernandiaceae (Laurales), and the egg, larva, and pupa are papilionid-like (HOWARTH, 1976). *Lamproptera* shows the greatest departure from the normal papilionid form. The smooth, spherical eggs of Papilionidae and Hesperidae are quite similar and both have similar genital muscles (STEKOL'NIKOV, 1967). A close relationship between Hesperidae and Papilionidae is emphasized by some authors (cf. GROTE, 1899), and cladistically Papilionidae arose from Hesperidae (KRISTENSEN, 1976).

Recent classifications of Papilionidae invariably place *Baronia* in the primitive, basal position (RICHARD & GUEDES, 1983; OKANO, 1983; HANCOCK, 1983; IGARASHI, 1984; SCOTT, 1984; MILLER, 1987). However, fossil pollen of *Acacia*, its larval foodplant, first appeared during the mid-Upper Eocene, and the earliest Fabales are only mid-Maestrictian in age (MULLER, 1984). *Acacia* belongs to the subfamily Mimosoideae which first entered the fossil record as a primitive, extinct genus at the Paleocene-Eocene boundary in Tennessee (CREPET & TAYLOR, 1985). Six species of *Acacia* occurred in western North America during Eocene times (LAMOTTE, 1952).

Laurales

Lamproptera is very close to *Graphium* in egg, first instar larva, and pupa, though slightly differing in venation (IGARASHI, 1984). In Papilionidae, anthoxanthins are most widespread in *Lamproptera* and *Graphium* (FORD, 1941). Ranales larval foodplants for *Graphium* include Monimiaceae, Lauraceae, Hernandiaceae, Winteraceae, Annonaceae, and Magnoliaceae. Core Laurales families of the *Euschemon*-Pyrginae-*Lamproptera*-*Graphium* relationship are Monimiaceae, Lauraceae, and Hernandiaceae.

The Monimiaceae, Lauraceae, and Hernandiaceae are clearly related (CRONQUIST, 1981). Monimiaceae and Lauraceae are closely related by cladistics, and Monimiaceae, Lauraceae, and Hernandiaceae are closely related by wood anatomy, pollen, and embryology (SASTRI, 1969; WALKER, 1976a; DAHLGREN & BREMER, 1985). Monimiaceae and Hernandiaceae both have longitudinal dehiscence of anthers, and in *Illigera* of Hernandiaceae the spine morphology of the pollen is similar to some Monimiaceae (SASTRI, 1969; WALKER, 1976b). Monimiaceae is primitive within Laurales, with the

relatives of most of the other Laurales families leading back to Monimiaceae; Lauraceae originated from primitive members of Monimiaceae (CRONQUIST, 1981).

Monimiaceae is known from Albian fossil pollen and from fossil woods and leaves from the Upper Cretaceous (CRONQUIST, 1981; MULLER, 1984). Lauraceae fossils first appear as leaf and fruit remains from the Albian of Far Eastern Russia and Western Canada (SAMYLINA, 1968). The Laurales family Chloranthaceae and Monimiaceae have conspicuously wide rays, similar hypodermis, stomata, unilacunar nodes, and stamens (SWAMY, 1953). *Hedyosmum* of Chloranthaceae is a "living fossil" in possessing a cone-like male flower perfectly homologous to the simple male gymnosperm cone, and *Sarcandra* has very primitive, gymnospermous wood (LEROY, 1983). Chloranthaceae is sometimes considered a separate order, Chloranthales. Pollen of *Hedyosmum* and *Ascarina* (Chloranthaceae) closely correspond with *Clavatipollenites* fossil pollen in gross morphology (DAHLGREN & BREMER, 1985; WALKER, 1976b; LEROY, 1983; WALKER & WALKER, 1984). Chloranthaceae flowers that combined characters of modern *Chloranthus* and *Sarcandra* occur in the early Late Albian of Maryland (FRIIS, CRANE, & PEDERSEN, 1986). The distribution of *Ascarina*, *Hedyosmum*, *Chloranthus*, and *Sarcandra* overlaps in Indomalaysia. *Clavatipollenites* is the first Laurales to enter the fossil record (mid-Barremian of England, Maryland, Gabon and Argentina). *Clavatipollenites* first appeared in Australia during the Albian (DETTMAN, 1973). Monimiaceae and *Euschemon* probably first arose during the Albian, 113–97.5 Myr ago.

Moth ancestors

The Lymantriidae are placed in the Noctuoidea near Noctuidae (including Agaristidae) on the basis of a general uniformity of structure and the presence of a tympanum (TUTT, 1899; BROCK, 1971); Euteliinae Noctuidae larvae are similar to Arctiidae and Lymantriidae (FORBES, 1960). Noctuoidea is the least structurally divergent and the most advanced superfamily of ditrysian moths (BROCK, 1971; HEPPNER, 1977). The antennae of Agaristidae, Noctuidae, and Lymantriidae are very similar in structure and show considerable variation (BODINE, 1896). Lymantriidae evolved from Hypsidae which have similar primitive venation; Hypsidae is the linking family between Noctuidae and Lymantriidae based on head structure (HAMPSON, 1898; FORBES, 1923; TURNER, 1947). The widespread phenomenon of "hilltopping" in Rhopalocera is present in diurnal moths only in the Agaristidae (SHIELDS, 1967; McFARLAND, 1976) and in Noctuidae and Cochlidae of nocturnal moths (WELLING, 1958). This is an example of a complex behavioral character (WILEY, 1981). Cyanogenesis and upright eggs are mostly confined to Rhopalocera and other advanced Ditrysia (TUTT, 1899; WITTHOLN & NAUMANN, 1987). The Madagascar agaristids *Pemphigostola* and *Musurgina* evidently evolved from advanced Castniidae (STRAND, 1930; KIRIAKOFF & VIETTE, 1974). *Pemphigostola* has antennal structure and forewing venation like *Synemon* castniids (Synemoninae), and *Musurgina* is connected with castniids by venation peculiarities and with agaristids by many other characters such as color scheme and stridulation apparatus. *Synemon parthenoides* FELDER (extreme southern Australia) has the antennal club joined to a wide shaft as in *Pemphigostola* (STRAND, 1909).

Pemphigostola and *Musurgina* are similar in the peculiar antennae, the stridulating organs, and the size and shape of the wings (JORDAN, 1921). The Madagascar and Comores agaristid *Ancarista* strongly resembles Noctuidae in facies and antennae. Most authors agree that Agaristidae and Noctuidae are closely related, and some include Agaristidae as a subfamily of Noctuidae (COMMON, pers. comm.). *Musurgina* and *Ancarista* have a similar protruding frons. Precise localities and illustrations of male and female genitalia and adults for *Pemphigostola*, *Musurgina*, and *Ancarista* appear in KIRIAKOFF and VIETTE (1974). Unfortunately the immature stages and foodplants are unknown. The agaristid *Saigonita* from Saigon, southern South Vietnam, displays a striking resemblance to *Pemphigostola* in male genitalia, male antennae clubbed, size, coloration, and facies and must have been anciently linked with it, though *Saigonita* differs somewhat in certain features of venation and male genitalia, male forewing shape, and in its less-elaborate stridulatory organ (KIRIAKOFF, 1971) as would be expected from such a disjunct distribution.

Noctuoidea and Geometroidea have similar venational trends, tympanum, and unprotected pupae. Hooked antennae are present in agaristids, pyrgines, *Apoprogon*es, and certain Uraniidae, and hesperiid and papilionid convergent forms both occur in Uraniidae. Uraniidae and Agaristidae, combined by some early workers, are similar in antennal shape and the armature of the posterior tibia. *Apoprogon*es of Apoprogonidae (Zululand and Transvaal) near Uraniidae links with Hemitheinae Geometridae by venation and transverse markings.

It does not appear possible to derive Rhopalocera directly from Castniidae (see SCOTT, 1986b) because of drastic differences in venation and aorta, although certain parallels exist such as day-flying, territoriality, clubbed antennae, and color patterns. Castniidae differ from Hesperidae in eye ring structure, in antennae located very close together, and in venation (TURNER, 1947; MILLER, 1970). Similarities in male genitalia, archaic venation, larvae, and pupae unite Castniidae and Cossidae as the Cossiformes group (LAMEERE, 1936; NICULESCU, 1970). Castniidae have advanced over Cossidae in possessing clubbed antennae, colorful wings, well-developed proboscis, diurnal flight, territorial behavior, and a well-developed frenulum. It would appear that most of the diurnal Lepidopteran families ultimately were derived from Castniidae. Metarbelidae of Cossioidea produced Psychidae of Bombycoidea via the morphologically intermediate genus *Psychidarbela* (Psychidarbelinae) of central Java (ROEPKE, 1938). Psychidae and Zygaenidae are close in male genitalia (MEHTA, 1933).

The date for the origin of Castniidae can be approximately determined. Castniidae foodplants are strictly monocots, on Palmae, Liliaceae, Amaryllidaceae, Iridaceae, Bromeliaceae, Marantaceae, Heliconiaceae, Musaceae, Orchidaceae, Cyperaceae, and Gramineae. The first extant monocot fossils were Araceae (Bathonian, Middle Jurassic) and Liliaceae (Early Oxfordian, lower Upper Jurassic) of England (SHIELDS, 1988). By Neocomian-Aptian times, Potamogetonaceae, Sparganiaceae, Cyperaceae, and Gramineae had appeared in Gobi, Mongolia (KRASSILOV, 1984). Madagascar with *Pemphigostola* first separated from Australia and Africa during mid-Oxfordian, lower Upper Jurassic, ca. 160 Myr ago (OWEN, 1983; KENT & GRAD-

STEIN, 1985; COFFIN & RABINOWITZ, 1987). The Indo-Australian castniids are more advanced than the Neotropical Castniinae in morphology.

Monotrysia includes all homoneurous and heteroneurous Micro-lepidoptera with a single genital opening in the female, while Ditrysia includes all heteroneurous Lepidoptera with two genital openings and an internal ductus seminalis (endoporian) in the female (COMMON, 1975). Exoporia (Mnesarchaeoidea and Hepialoidea) is intermediate between Monotrysia and Ditrysia in being homoneurous with two genital openings and an external ductus seminalis (exoporian) in the female (DUMBLETON, 1966; NIELSEN, 1985). Exoporia are also characterized by their wing scales having dimorphic longitudinal ridges (KRISTENSEN, 1978). Hepialoidea and Ditrysia have a dorsal common oviduct which is ventral in Monotrysia (DUGDALE, 1974). The specialized family Opostegidae of Monotrysia possesses one or two genital openings in the female (DUGDALE, 1974).

Hepialidae and Cossidae share a number of similarities. Their larvae live in tunnels, construct trap-doors, and have scutellar depressions. A cocoon is spun within the tunnel in hepialids and some cossids. The pupae are spined and protrude from the tunnels at ecdysis, also in Castniidae (see HINTON, 1948; SCOTT, 1986b). Adults are highly fecund and possess similar distinctive wing patterns. In both the haustellum is vestigial or absent and venation is fairly similar (hepialid venation is homoneurous but with a slight heteroneurous tendency). In the male genitalia the harpes, juxta, and aedeagus are closely associated or fused. Some workers have been more impressed by their differences than their similarities (e.g. jugum vs. frenulum, ventral proleg crochets arrangement, etc.). However, in sum the differences do not outweigh the similarities, differences would be expected in such an ancient relationship, and most differences could have resulted from cossid specializations (see below). Hepialidae have some modified holding scales on the anterior border of the hindwing, perhaps the first stage of the frenulum condition (FRIESE, 1970). There are clear affinities in numerous Ditrysiian families to Cossidae venation (TURNER, 1918), so that its basal, ancestral position within Ditrysia appears secure. Ditrysiian phylogeny is outlined in Figure 1.

Hepialidae is the most advanced, successful, and specialized family of Exoporia. Mnesarchaeidae is endemic to New Zealand and Hepialoidea (sans Hepialidae) is restricted to Gondwanaland continents. Hepialidae is cosmopolitan with the most primitive genera in the Australian region. Cossidae, the most primitive family of Ditrysia, is cosmopolitan with the most primitive genera in the Ethiopian region. Castniidae is confined to the Australian, Oriental, and Neotropical regions with all primitive genera restricted to the Neotropical region. Agaristidae is nearly cosmopolitan with the most primitive genera of Madagascar and in the Oriental region; it most likely arose on Madagascar. These dispersals must have occurred prior to the breakup of Gondwanaland (cf. SHIELDS, 1977, 1979), progressing in a westward track across the southern continents (northern Gondwanaland) during the Jurassic.

Extinct late Palaeontinidae Homoptera of the Lower and Middle Jurassic of Central Asia and Siberia (cf. BEKKER-MIGDISOVA & WOOTTON, 1965) often strikingly

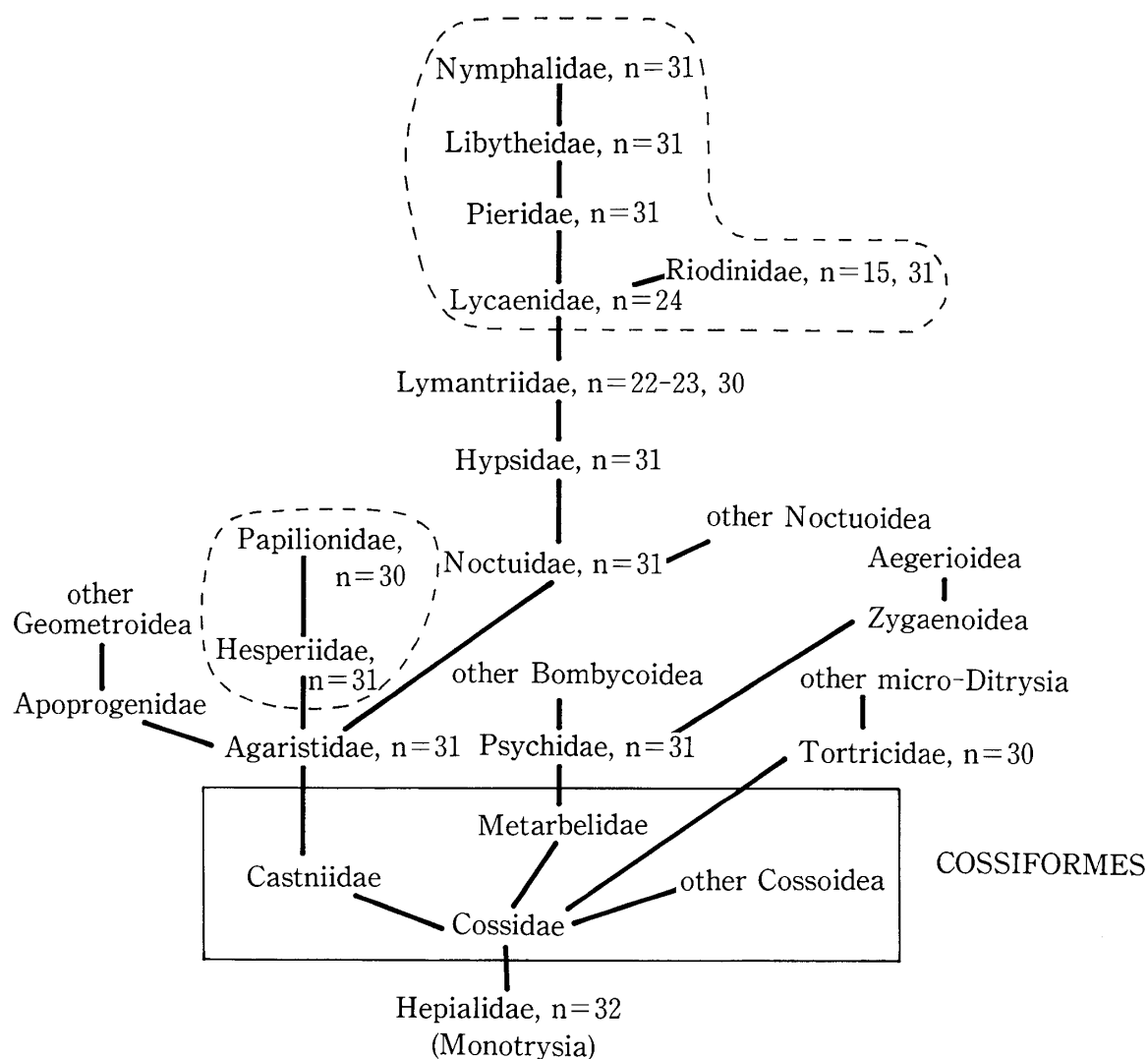


Figure 1. Proposed phylogeny of Ditrysia showing the diphyletic origin of Rhopalocera (most names *sensu* BROCK, 1971; HEPPNER, 1977). Evolutionary reversals (incongruent with other characters) include diurnal activity and clubbed antennae, modal haploid chromosome numbers (ROBINSON, 1971, etc.), micro-Ditrysia, and lek behavior. Lek behavior is also present in Hepialidae (MALLET, 1984). Though some authors link Tortricidae with Cossidae, Tineidae is closer to Cossidae in neuration and protruding pupa at ecdysis (cf. TURNER, 1918; HEPPNER, 1977). The simplified, greatly reduced venation of Opostegidae and Tischeriidae removes these Heteroneura Monotrysia from consideration as precursors to micro-Ditrysia. Deriving Tineoidea from the Incuvarioidea or Palaephatidae Monotrysia (DAVIS, 1986) encounters fundamental problems of two vs. one female genital apertures, dorsal vs. ventral common oviduct (see DUGDALE, 1974), and nonaculeate vs. aculeate wings.

resemble certain larger Cossidae in size, robust bodies, sound production (cf. EVANS, 1957; COMMON, 1969), wing shape and pattern, and venation. They of course differ from Cossidae in being homopteran and in possessing granulations instead of scales, usually an extra marginal vein, well-developed proboscis, etc. Cossidae may well have mimicked these Palaeontinidae in time and space. The first undisputed lepidopteran fossil (*Archaeolepis* of Aglossata) comes from the lower Lower Jurassic of England (WHALLEY, 1986). Lepidoptera likely arose from extinct Necrotauliidae Trichoptera at the Triassic/Jurassic boundary (SHIELDS, 1988).

From detailed cladistic analyses, Mnesarchaeidae of Exoporia arose from the archaic, homoneurous, sister family Neopseustidae of Neopseustina (NIELSEN, 1982, 1985; KRISTENSEN, 1984). Neopseustidae has a disjunct distribution in Assam, Burma, Szechwan, and Taiwan, and south-central Chile and the adjacent Andes of Argentina with the most primitive genera in the Oriental region.

The evolutionary sequence of Rhopaloceran families outlined here strictly obeys Cope's Rule, i.e. the widespread tendency of animals to evolve toward larger physical size (STANLEY, 1973). In Hesperidae and Papilionidae, the apophyseal retractor muscles of the 9th segment extend to the 7th tergite, while in all other Rhopaloceran families these muscles extend to the 8th segment (STEKOL'NIKOV, 1967), adding support to the diphyletic origin of Rhopalocera proposed here. The Agaristidae-Hesperidae – Papilionidae series was a northward advancement, from Queensland to throughout the Oriental region. The Lymantriidae – Lycaenidae – Pieridae – Libytheidae – Nymphalidae series was a westward advancement, from Africa through the Caribbean – Central America – Mexico region to the Orient. Both paths are restricted to Gondwanaland.

Acknowledgements

I thank P. A. ADAMS, F. M. BROWN, T.J. COHN, I.F.B. COMMON, C.F. COWAN, J.P. DONAHUE, P.R. EHRLICH, T.C. EMMEL, T.P. FRIEDLANDER, N.P. KRISTENSEN, N. MCFARLAND, L.D. and J.Y. MILLER, E.M. PERKINS, A. RYDON, J.A. SCOTT, A.M. SHAPIRO, S.R. SIMS, N.B. TINDALE, P. VIETTE, D. WAGNER, G.L. WEBSTER, R.E. WELLS, P.E.S. WHALLEY, and R. WOOTTON for helpful discussions and/or correspondence, and especially T.J. COHN and L.D. MILLER for guidance in preparing the paper.

References

- ACKERY, P.R., 1984. Systematics and faunistic studies of butterflies. *Symposia R. ent. Soc. Lond.*, **11**: 9 – 21.
- & R.I. VANE-WRIGHT, 1984. *Milkweed Butterflies: their Cladistics and Biology*. Br. Mus. (Nat. Hist.), London.
- AOKI, T., YAMAGUCHI, S. & Y. UEMURA, 1982. *Butterflies of the South East Asian Islands, vol. 3. Satyridae, Libytheidae*. Palapac, Tokyo.
- ARNOLD, E.N., 1981. Estimating phylogenies at low taxonomic levels. *Zeit. Zool. Syst. Evol.*, **19**: 1 – 35.
- ASHIZAWA, H. & Y. MUROYA, 1967. Notes on the early stages of *Calinaga buddha formosana* FRUHSTORFER. *Spec. Bull. Lep. Soc. Jap.*, **3**: 79 – 89.
- ASHLOCK, P.D., 1979. An evolutionary systematist's view of classification. *Syst. Zool.*, **28**: 441 – 450.
- AURIVILLIUS, C., 1919. Family Erycinidae. In A. SEITZ (Ed.), *The Macrolepidoptera of the World. The*

- African Rhopalocera*, vol.13: 293–294. A. Kernen, Stuttgart.
- AX P., 1985. Stem species and the stem lineage concept. *Cladistics*, **1**: 279–287.
- BALDUF, W.V., 1939. *The Bionomics of Entomophagous Insects*, part 2. J.S. Swift, St. Louis.
- BATES, M., 1932. Notes on the metamorphosis of the Brassolidae. *Bull. Brook. ent. Soc.*, **27**: 155–163.
- 1935. The butterflies of Cuba. *Bull. Mus. Comp. Zool., Harvard Univ.*, **78**: 63–258.
- BEATTY, J., 1982. Classes and cladists. *Syst. Zool.*, **31**: 25–34.
- BEESON, C.F.H., 1941. *The Ecology and Control of the Forest Insects of India and the Neighbouring Countries*. Reprinted 1961 by the Government of India.
- BEKKER-MIGDISOVA, E.E. & R. WOOTTON, 1965. New Palaeontinidae from Asia. *Paleont. Zhur., Moscow*, **2**: 63–79. (In Russian.)
- BELL, T.R., 1910. The common butterflies of the plains of India, part 8. *J. Bombay nat. Hist. Soc.*, **20**: 279–329.
- BERG, C.C., 1977. Urticales, their differentiation and systematic position. *Plant Syst. Evol., Suppl.*, **1**: 349–374.
- BOCK, W.J., 1968. Phylogenetic systematics, cladistics and evolution. *Evolution*, **22**: 646–648.
- 1977. Foundations and methods of evolutionary classification. In M.K. HECHT, P.C. GOODY & B.M. HECHT (Eds.), *Major Patterns in Vertebrate Evolution*: 851–895. Plenum Press, New York and London.
- 1979. The synthetic explanation of macroevolutionary change — a reductionistic approach. *Bull. Carnegie Mus. nat. Hist.*, **13**: 20–69.
- BODINE, D., 1896. The taxonomic value of the antenna of the Lepidoptera. *Trans. Amer. ent. Soc.*, **23**: 1–56, 5 pls.
- BREMER, K., 1985. Summary of green plant phylogeny and classifications. *Cladistics*, **1**: 369–385.
- BROCK, J.P., 1971. A contribution towards an understanding of the morphology and phylogeny of the Ditrysian Lepidoptera. *J. nat. Hist.*, **5**: 29–102.
- BROOKS, D.R. & E.O. WILEY, 1985. Theories and methods in different approaches to phylogenetic systematics. *Cladistics*, **1**: 1–11.
- BROWER, L.P. & J.V. BROWER, 1972. Parallelism, convergence, divergence, and the concept of advergence in the evolution of mimicry. *Trans. Connecticut Acad. Arts Sci.*, **44**: 57–67.
- BROWN, F.M. & B. HEINEMAN, 1972. *Jamaica and its Butterflies*. E.W. Classey Ltd., London.
- BROWN, T.M. & K.D. ROSE, 1987. Patterns of dental evolution in Early Eocene Anaptomorphine primates (Omomyidae) from the Bighorn Basin, Wyoming. *Paleo. Soc. Mem.*, **23**: 1–162.
- BRYK, F., 1934. Lymantriidae. *Lep. Catalogus*, **62**: 1–441.
- BUTLER, A.G., 1871. Descriptions of a new genus and six new species of Pierinae. *Trans. ent. Soc. Lond.*, 1871 (part 2): 169–173, 1 pl.
- CAIN, A.J. & G.A. HARRISON, 1960. Phyletic weighting. *Proc., zool. Soc. Lond.*, **135**: 1–31.
- CHAPMAN, T.A., 1895. Notes on butterfly pupae, with some remarks on the phylogenesis of the Rhopalocera. *Ent. Rec. J. Var.*, **6**: 101–107, 125–131, 147–152.
- 1900a. Some points in the evolution of the lepidopterous antenna. *Trans. Proc. South Lond. Ent. nat. Hist. Soc.*, **1900**: 1–19.
- 1900b. The pupa of *Libythea celtis*. *Ent. Rec. J. Var.*, **12**: 284–286.
- 1912. *Libythea celtis*. Eggs and oviposition. *Ent. Rec. J. Var.*, **24**: 302–303.
- CLARK, A.H., 1947. The interrelationships of the several groups within the butterfly superfamily Nymphaloidea. *Proc. ent. Soc. Washington*, **49**: 148–149.
- 1948. Classification of the butterflies, with the allocation of the genera occurring in North America north of Mexico. *Proc. biol. Soc. Washington*, **61**: 77–84.
- CLARK, G.C. & C.G.C. DICKSON, 1964. The life history of *Libythea labdaca laius* Trimen. *J. ent. Soc. Southern Africa*, **26**: 290–292, 1 pl.
- CLENCH, H.K., 1955. Revised classification of the butterfly family Lycaenidae and its allies. *Ann. Carnegie Mus.*, **33**: 261–274.
- COFFIN, M.F. & P.D. RABINOWITZ, 1987. Reconstruction of Madagascar and Africa: evidence from the

- Davie Fracture Zone and western Somali Basin. *J. geophys. Res.*, **92**: 9385–9406.
- COLLENETTE, C.L., 1953. The family Lymantriidae. *Entomologist*, **86**: 32–33.
- COMMON, I.F.B., 1969. A wing-locking or stridulatory device in Lepidoptera. *J. Austral. ent. Soc.*, **8**: 121–125.
- 1975. Evolution and classification of the Lepidoptera. *Ann. Rev. Ent.*, **20**: 183–203.
- & D.F. WATERHOUSE, 1972. *Butterflies of Australia*. Angus & Robertson, Sydney.
- COMSTOCK, J.A., 1927. *Butterflies of California*. Los Angeles: published by the author.
- & L.V. GARCIA, 1960. Estudios de los ciclos biológicos en Lepidópteros Mexicanos. *An. Inst. Biol. Univ. México*, **31**: 349–448.
- COMSTOCK, W.P., 1944. Insects of Porto Rico and the Virgin Islands: Rhopalocera or butterflies. *New York Acad. Sci., Scientific Survey of Porto Rico and the Virgin Islands*, **12**(4): 421–622.
- CORBET, A.S. & H.M. PENDLEBURY, 1978. *The Butterflies of the Malay Peninsula*, 3rd ed. Malayan Nature Society, Kuala Lumpur.
- CRANE, P.R., 1985. Phylogenetic relationships in seed plants. *Cladistics*, **1**: 329–348.
- CREPET, W.L. & D.W. TAYLOR, 1985. The diversification of the Leguminosae: first fossil evidence of the Mimosoideae and Papilionoideae. *Science*, **228**: 1087–1089.
- CRISCI, J.V. & T.F. STUESSY, 1980. Determining primitive character states for phylogenetic reconstruction. *Syst. Bot.*, **5**: 112–135.
- CRONQUIST, A., 1981. *An Integrated System of Classification of Flowering Plants*. Columbia University Press, New York.
- DAHLGREN, R. & K. BREMER, 1985. Major clades of the angiosperms. *Cladistics*, **1**: 349–368.
- DAVIS, D.R., 1986. A new family of monotrysian moths from austral South America (Palaephatidae), with a phylogenetic review of the Monotrysia. *Smithsonian Cont. Zool.*, **434**: 1–202.
- DEGTYAREVA, V.I., 1961. Materials on the geographical distribution and biology of the nettle-tree butterfly (*Libythea celtis* Esp.) in Tadzhikistan. *Akademiia nauk Tadzhikskoi SSR, Stalinabad; Otdelnie sel'skokhoziaistvennykh i biologicheskikh nauk, Izvestiia*, **1**(4): 115–119 (in Russian).
- DETTMANN, M.E., 1973. Angiospermous pollen from Albian to Turonian sediments of eastern Australia. *Geol. Soc. Austral., Spec. Publ.*, **4**: 3–34.
- DE VRIES, P.J., KITCHING, I.J. & R.I. VANE-WRIGHT, 1985. The systematic position of *Antirrhea* and *Caerois*, with comments on the classification of the Nymphalidae. *Syst. Ent.*, **10**: 11–32.
- DICKSON, C.G.C. & D.M. KROON, 1978. *Pennington's Butterflies of Southern Africa*. AD. Donker, Johannesburg.
- DIXEY, F.A., 1894. On the phylogeny of the Pierinae, as illustrated by their wing-markings and geographical distribution. *Trans. ent. Soc. Lond.*, **42**: 249–334, 3 pls.
- 1910. The plume-scales of the Pierinae. *Trans. ent. Soc. Lond.*, **1910**: 1–55.
- DOWNEY, J.C., 1966. Sound production in pupae of Lycaenidae. *J. Lep. Soc.*, **20**: 129–155.
- & A.C. ALLYN, 1973. Butterfly ultrastructure. 1. Sound production and associated abdominal structures in pupae of Lycaenidae and Riodinidae. *Bull. Allyn Mus.*, **14**: 1–47.
- DUGDALE, J.S., 1974. Female genitalia configuration in the classification of Lepidoptera. *New Zealand J. Zool.*, **1**: 127–146.
- DUMBLETON, L.J., 1966. Genitalia, classification and zoogeography of the New Zealand Hepialidae. *New Zealand J. Sci.*, **9**: 920–981.
- DURDEN, C.J. & H. ROSE, 1978. Butterflies from the Middle Eocene: the earliest occurrence of fossil Papilionoidea (Lepidoptera). *Pearce-Sellards Series, Texas Mem. Mus.*, **29**: 1–25.
- EDWARDS, W.H., 1884. *The Butterflies of North America*, vol.2. Boston: Houghton, Mifflin & Co.
- EHRlich, P.R., 1958a. The comparative morphology, phylogeny and higher classification of the butterflies. *Univ. Kansas Sci. Bull.*, **39**: 305–370.
- 1958b. A note on the systematic position of the butterfly genus *Calinaga* (Nymphalidae). *Lepidopterist's News*, **12**: 173.
- & A.H. EHRlich, 1961. *How to know the Butterflies*. W.C. Brown, Dubuque.

- & ——— 1967. The phenetic relationships of the butterflies I. Adult taxonomy and the nonspecificity hypothesis. *Syst. Zool.*, **16**: 301–317.
- & P.H. RAVEN, 1965. Butterfly and plants: a study in coevolution. *Evolution*, **18**: 586–608.
- ELDRIDGE, N. & M.J. NOVACEK, 1985. Systematics and paleobiology. *Paleobiology*, **11**: 65–74.
- & S.M. STANLEY (Eds.), 1984. *Living Fossils*. Springer Verlag, New York.
- ELIOT, J.N., 1973. The higher classification of the Lycaenidae: a tentative arrangement. *Bull. Br. Mus. nat. Hist. (Ent.)*, **28**: 373–505, 6 pls.
- ELTRINGHAM, H., 1922. On the species of the genus *Larinopoda* BUTLER. *Trans. ent. Soc. Lond.*, **1922**: 254–268, 2 pls.
- ENGELMANN, G.F. & E.O. WILEY, 1977. The place of ancestor-descendant relationships in phylogeny reconstruction. *Syst. Zool.*, **26**: 1–11.
- ESTABROOK, G.F., 1977. Does common equal primitive? *Syst. Bot.*, **2**: 36–42.
- EVANS, J.W., 1957. Some aspects of the morphology and interrelationships of extinct and recent Homoptera. *Trans. R. ent. Soc. Lond.*, **109**: 275–294.
- EVANS, W.H., 1949. *A Catalogue of the Hesperidae from Europe, Asia and Australia in the British Museum (Natural History)*. Jarrold & Sons, Norwich.
- 1955. *A Catalogue of the American Hesperidae in the British Museum (Natural History)*. Part IV. *Hesperinae and Megathyminae*. Jarrold & Sons, Norwich.
- EYDE, R.H., 1971. Evolutionary morphology: distinguishing ancestral structure from derived structure in flowering plants. *Taxon*, **20**: 63–73.
- FARRIS, J.S., 1977. Phylogenetic analysis under DOLLO's Law. *Syst. Zool.*, **26**: 77–88.
- FIELD, W.D., 1938. A manual of the butterflies and skippers of Kansas. *Bull. Univ. Kansas*, **39** (10): 1–328, 2 pls.
- FISHER, D.C., 1981. The role of functional analysis in phylogenetic inference: examples from the history of the Xiphosura. *Amer. Zool.*, **21**: 47–62.
- FORBES, W.T.M., 1923. The Lepidoptera of New York and neighboring states. *Cornell Univ. Agr. Exp. Station Mem.*, **68**: 1–729.
- 1960. Lepidoptera of New York and neighboring states. Part 4. Agaristidae through Nymphalidae including butterflies. *Cornell Univ. Agr. Exp. Station Mem.*, **371**: 1–188.
- FORD, E.B., 1941. Studies on the chemistry of pigments in the Lepidoptera, with reference to their bearing on systematics. 1. The anthoxanthins. *Proc. R. Ent. Soc. Lond. (A)*, **16**: 65–90.
- FORSTER, W., 1964. Beitrage zur Kenntnis der Insektenfauna Boliviens 19. Lepidoptera 3. *Veröff. Zool. Staat.*, **8**: 51–188.
- FRACKER, S.B., 1915. The classification of lepidopterous larvae. *Illinois biol. Monographs*, **2** (1): 1–169.
- FRIEDLANDER, T.P., 1984. Another look at snout butterflies (Libytheidae: *Libytheana*). *J. Soc.*, **38**: 139–141.
- FRIESE, G., 1970. Zur Phylogenie der älteren Teilgruppen der Lepidopteren. *Wander. Deutsch. Ent.*, **80**: 203–222.
- FRIIS, E.M., CRANE, P.R. & K.R. PEDERSEN, 1986. Floral evidence for Cretaceous chloranthoid angiosperms. *Nature*, **320**: 163–164.
- FRUHSTORFER, H., 1914. Erycinidae, *Libythea*. In A. SEITZ (ed.), *The Macrolepidoptera of the World*, vol. 9. *The Indo-Australian Rhopalocera*: 767–771. A. Kernen, Stuttgart.
- GALL, L.F. & B.H. TIFFNEY, 1983. A fossil noctuid moth egg from the Late Cretaceous of eastern North America. *Science*, **219**: 507–509.
- GINGERICH, P.D., 1979. The stratophenetic approach to phylogeny reconstruction in vertebrate paleontology. In J. CRACRAFT & N. ELDRIDGE (Eds.), *Phylogenetic Analysis and Paleontology*: 41–77. Columbia University Press, New York.
- GODMAN, F.D. & O. SALVIN, 1879–1901. *Biologia Centrali-Americana. Insecta. Lepidoptera-Rhopalocera*, vol. 1. R.H. Porter, London.
- GOULD, S.J., 1970. DOLLO on DOLLO's Law: irreversibility and the status of evolutionary laws. *J. Hist. Biol.*, **3**: 189–212.

- GROTE, A.R., 1898. Specializations of the lepidopterous wing; the pieri-nymphalidae. *Proc. Amer. philosoph. Soc.*, **37**: 17–44, 3 pls.
- 1899. Genealogical trees of butterflies. *Proc. Amer. philosoph. Soc.*, **38**: 147–154.
- 1900. The descent of the pierids. *Proc. Amer. philosoph. Soc.*, **39**: 4–67, 4 pls.
- HAMPSON, G.F., 1898. *Catalogue of the Lepidoptera Phalaenae in the British Museum*, vol. 1. Printed by order of the trustees, London.
- HANCOCK, D.L., 1983. Classification of the Papilionidae (Lepidoptera): a phylogenetic approach. *Smithersia*, **2**: 1–48.
- HARPER, C.W., Jr., 1976. Phylogenetic inference in paleontology. *J. Paleont.*, **50**: 180–193.
- HEADS, M., 1985. On the nature of ancestors. *Syst. Zool.*, **34**: 205–215.
- HECHT, M.K., 1976. Phylogenetic inference and methodology as applied to the vertebrate record. *Evol. Biol.*, **9**: 335–363.
- & J.L. EDWARDS, 1976a. The methodology of phylogenetic inference above the species level. In M.K. HECHT, P.C. GOODY & B.M. HECHT (Eds), *Major Patterns in Vertebrate Evolution*: 3–51. Plenum Press, New York and London.
- & ——— 1976b. The determination of parallel or monophyletic relationships: the proteid salamanders—a test case. *Amer. Nat.*, **110**: 653–677.
- HENNING, S.F., 1983. Biological groups within the Lycaenidae. *J. ent. Soc. south. Africa*, **46** (1): 65–85.
- HEPPNER, J.B., 1977. The status of the Glyphipteridae and a reassessment of relationships in yponomeutoid families and ditrysian superfamilies. *J. Lep. Soc.*, **31**: 124–134.
- HESSEL, J.H., 1966. A preliminary comparative anatomical study of the mesothoracic aorta of the Lepidoptera. *Ann. ent. Soc. Amer.*, **59**: 1217–1227.
- 1969. The comparative morphology of the dorsal vessel and accessory structures of the Lepidoptera and its phylogenetic implications. *Ann. Ent. Soc. Amer.*, **62**: 353–370.
- HEYWOOD, V.H., 1977. Principles and concepts in the classification of higher taxa. *Plant Syst. Evol., Suppl.*, **1**: 1–12.
- HIGGINS, L.G., 1975. *The Classification of European Butterflies*. Collins, London.
- HINTON, H.E., 1948. Sound production in lepidopterous pupae. *Entomologist*, **81**: 254–269.
- 1951. Myrmecophilous Lycaenidae and other Lepidoptera—a summary. *Proc. Trans. south Lond. ent. nat. Hist. Soc.*, **1941/1950**: 111–175.
- HOLLAND, W.J., 1955. *The Butterfly Book*, revised ed. Doubleday, Garden City.
- HOLMQUIST, R., 1979. The method of parsimony: an experimental test and theoretical analysis of the adequacy of molecular restoration studies. *J. Mol. Biol.*, **135**: 939–958.
- HOMMA, T., 1954. A comparative study of the alimentary canal in butterflies, with special reference to their systematic relationships. *J. Fac. Sci., Hokkaido Univ., Ser. 6, Zool.*, **12**: 40–60.
- HOWARTH, T.G., 1976. Notes on the biology of *Lamproptera curius walkeri* Moore. *J. Res. Lep.*, **15**: 27–32.
- IGARASHI, S., 1984. The classification of the Papilionidae mainly based on the morphology of the immature stages. *Tyô to Ga*, **34**: 41–96.
- JARZEMBOWSKI, E.A., 1980. Fossil insects from the Bembridge Marls, Palaeogene of the Isle of Wight, southern England. *Bull. Br. Mus. nat. Hist. (Geol.)*, **33**: 237–293.
- JOHNSON, K. & E.L. QUINTER, 1982. Commentary on Miller and Brown vs. Ehrlich and Murphy *et al.*: pluralism in systematics and the worldwide nature of kinship groups. *J. Res. Lep.*, **21**: 255–269.
- JOHNSON, R., 1982. Parsimony principles in phylogenetic systematics: a critical re-appraisal. *Evol. Biol.*, **6**: 79–90.
- JORDAN, K., 1898. Contributions to the morphology of Lepidoptera. *Novit. Zool.*, **5**: 374–415, 2 pls.
- 1921. On the replacement of a lost vein in connection with a stridulating organ in a new agaristid moth from Madagascar, with descriptions of two new genera. *Novit. Zool.*, **28**: 68–74.
- 1925. Über die Stellung der Tagfaltergattung *Libythea*. *Third Int. Congr. Ent., Zurich*: 361–366.

- KAWAZOE, A. & M. WAKABAYASHI, 1976. *Coloured Illustrations of the Butterflies of Japan*, revised ed. Hoikusha, Osaka. (In Japanese.)
- KENNEDY, W.J., & M. COOPER, 1975. Cretaceous ammonite distributions and the opening of the South Atlantic. *J. geol. Soc. Lond.*, **131**: 283–288.
- KENT, D.V. & F.M. GRADSTEIN, 1985. A Cretaceous and Jurassic geochronology. *Geol. Soc. Amer. Bull.*, **96**: 1419–1427.
- KIRIAKOFF, S.G. 1971. *Saigonita paradoxa* gen. nov. sp. nov. (Lepidoptera: Agaristidae) d'Indochine. *Lambillionea*, **71** (1–2): 5–11.
- & P. VIETTE, 1974. Insectes Lepidopteres Agaristidae. *Faune de Madagascar*, **39**: 1–122.
- KLOTS, A.B., 1930. A generic revision of the Euchloini. *Bull. Brook. ent. Soc.*, **25**: 80–95.
- 1931. A generic revision of the Pieridae, together with a study of the male genitalia. *Ent. Amer.*, **12**: 139–242, 9 pls.
- KRASSILOV, V.A., 1984. New paleobotanical data on origin and early evolution of angiosperms. *Ann. Missouri bot. Garden*, **71**: 577–592.
- KRISTENSEN, N.P., 1976. Remarks on the family-level phylogeny of butterflies. *Zeit. Zool. Syst. Evol.*, **14**: 25–33.
- 1978. Ridge dimorphism and second-order ridges on wing scales in Lepidoptera: Exoporia. *Int. J. Insect Morph. Embryol.*, **7**: 297–299.
- 1984. Studies on the morphology and systematics of primitive Lepidoptera. *Steenstrupia*, **10**: 141–191.
- KUSNEZOW, N., 1900. On the protective coloration and attitude of *Libythea celtis* Esp. *Vesesoiznoe Entomologicheskoe Obshchestvo*, **35**: 30–37. (In Russian.)
- LAMEERE, A., 1936. Évolution des Lépidoptères. *Bull. Ann. Soc. Ent. Belgique (Bruxelles)*, **76**: 407–413.
- LAMOTTE, R.S., 1952. Catalogue of the Cenozoic plants of North America through 1950. *Geol. Soc. Amer. Mem.*, **51**: 1–381.
- Le CERF, F., 1926. Contribution a l'étude des organes sensoriels des Lepidopteres. In P. Lechevalier (ed), *Encyclopedie Entomologique Ser. B, I. Lepidoptera, fasc. 3*: 133–158. Paris.
- LEECH, J.H., 1893. *Butterflies from China, Japan, and Corea*, part 3. R.H. Porter, London.
- LEESTMANS, R., 1983. Les Lépidoptères fossiles trouvés en France. *Linneana Belgica*, **9** (1): 64–89.
- Le QUESNE, W.J., 1974. The uniquely evolved character concept and its cladistic application. *Syst. Zool.*, **23**: 513–517.
- LEROY, J.-F., 1983. The origin of angiosperms: an unrecognized ancestral dicotyledon, *Hedyosmum* (Chloranthales), with a strobiloid flower is living today. *Taxon*, **31**: 169–175.
- de LESSE, H., 1967. Les nombres de chromosomes chez les Lepidopteres Rhopaloceres Neotropicaux. *Ann. Soc. Ent. France (n.s.)*, **3**(1): 67–136.
- McFARLAND, N., 1976. Hilltopping and defence behaviour in a diurnal agaristid moth. *Austral. Ent. Mag.*, **3**(2): 25–29.
- MALLET, J., 1984. Sex roles in the ghost moth *Hepialus humuli* (L.) and a review of mating in the Hepialidae. *Zool. J. Linn. Soc.*, **80**: 67–82.
- MAYR, E., 1974. Cladistic analysis or cladistic classification? *Zeit. Zool. Syst. Evol.*, **12**: 94–128.
- 1981. Biological classification: toward a synthesis of opposing methodologies. *Science*, **214**: 510–516.
- 1982. Speciation and macroevolution. *Evolution*, **36**: 1119–1132.
- MEARS, J.A., 1973. Chemical constituents and systematics of Amentiferae. *Brittonia*, **25**: 385–394.
- MEHTA, D.R., 1933. Comparative morphology of the male genitalia in Lepidoptera. *Rec. Ind. Mus.*, **35**: 197–266.
- MELVILLE, R., 1975. The distribution of Australian relict plants and its bearing on angiosperm evolution. *Bot. J. Linn. Soc.*, **71**: 67–88.
- MEYRICK, E., 1902. Revision of the Australian Hesperidae. *Trans. R. Soc. south Austral.*, **26**: 38–129.
- MICKEVICH, M.F., 1978. Taxonomic congruence. *Syst. Zool.*, **27**: 143–158.
- 1980. Taxonomic congruence: ROHLF and SOKAL's misunderstanding. *Syst. Zool.*, **29**: 162–

- 176.
- MILLER, J.S., 1987. Host-plant relationships in the Papilionidae: parallel cladogenesis or colonization? *Cladistics*, **3**: 105–120.
- MILLER, J.Y., 1970. The head capsule of selected Hesperioidea. *J. Res. Lep.*, **9**: 193–214.
- MILLER, L.D., 1968. The higher classification, phylogeny and zoogeography of the Satyridae. *Mem. Amer. Ent. Soc.*, **24**: 1–174.
- MILLER, W.H., BERNARD, G.D. & J.L. ALLEN, 1968. The optics of insect compound eyes. *Science*, **162**: 760–767.
- MULLER, J., 1968. Palynology of the Pedawan and Plateau sandstone formations (Cretaceous-Eocene) in Sarawak, Malaysia. *Micropaleontology*, **14**(1): 1–37, 5 pls.
- 1974. A comparison of SE Asia with European fossil angiosperm pollen floras. *Birbal Sahni Inst. Palaeobotany, Spec. Publ.*, **1**: 49–56.
- 1984. Significance of fossil pollen for angiosperm history. *Ann. Missouri Bot. Garden*, **71**: 419–443.
- MUNROE, E., 1949. The phylogeny of the Papilionidae. *Proc. 7th Pacific Sci. Congr.*, **4**: 83–87.
- 1960. The classification of the Papilionidae. *Can. Ent., Suppl.*, **17**: 1–51.
- NEFF, N.A., 1986. A rational basis for a priori character weighting. *Syst. Zool.*, **35**: 110–123.
- de NICÉVILLE, L., 1900. The foodplants of the butterflies of the Kanara district of the Bombay Presidency, with a revision of the species of butterflies there occurring. *J. Asiat. Soc. Beng.*, **69**: 187–278, 1 pl.
- NICULESCU, E.V., 1970. Aperçu critique sur le systématique et la phylogénie des Lépidoptères. *Bull. Soc. Ent. Mulhouse*, **1970**: 1–16.
- NIELSEN, E.S., 1982. Review of the higher classification of the Lepidoptera, with special reference to lower heteroneurans. *Tyô to Ga*, **33**: 98–101.
- 1985. Primitive (non-ditrysian) Lepidoptera of the Andes: diversity, distribution, biology and phylogenetic relationships. *J. Res. Lep., Suppl.*, **1**: 1–16.
- NOVACEK, M.J. & M.A. NORELL, 1982. Fossils, phylogeny, and taxonomic rates of evolution. *Syst. Zool.*, **31**: 366–375.
- OKANO, K., 1983. The revision of classification on the genera of Papilionidae in the world (preliminary report) Part I: with description of a new genus. *Tokurana (Acta Rhop.)*, **5**: 1–75.
- ORFILA, R.N., 1949. Notas sistematicas sobre Lepidoptera Rhopalocera. *Acta zool. Lilloana*, **8**: 583–586.
- 1950. Clasificación de Lepidoptera Rhopalocera. *Rev. Soc. Ent. Argentina*, **14**: 263–269.
- OWEN, H.G., 1983. *Atlas of Continental Displacement, 200 Million Years to the Present*. Cambridge University Press.
- PAGENSTECHE, A., 1901. Libytheidae. *Das Tierreich*, **14**: 1–18.
- PANCHEN, A.L., 1982. The use of parsimony in testing phylogenetic hypotheses. *Zool. J. Linn. Soc.*, **74**: 305–328.
- PATTERSON, C., 1980. Cladistics. *Biologist*, **27**: 234–240.
- 1982a. Morphological characters and homology. In K.A. Joysey & A.E. Friday (Eds.), *Problems of Phylogenetic Reconstruction*: 21–74. Academic Press, London.
- 1982b. Cladistics and classification. *New Scientist*, **94**: 303–306.
- PETERSON, A., 1962. *Larvae of Insects: an Introduction to Nearctic Species*, part 1, 4th ed. A. Peterson, Columbus, Ohio.
- POULTON, E.B., 1917. Mr. C. O. Farquharson's investigations into the life histories of S. Nigerian Lycaenidae. *Trans. ent. Soc. Lond.*, **65**: lxi–lxii.
- de QUEIROZ, K., 1985. The ontogenetic method for determining character polarity and its relevance to phylogenetic systematics. *Syst. Zool.*, **34**: 280–299.
- RAINBOW, W.J., 1907. *A Guide to the Study of Australian Butterflies*. Lothian, Melbourne.
- RAVEN, P.H., 1977. A suggestion concerning the Cretaceous rise to dominance of the angiosperms. *Evolution*, **31**: 451–452.

- REUTER, E., 1896. Über die Palpen der Rhopaloceren. *Acta Soc. Sci. Fennicae*, **24**: 1-577, 6 pls.
- REYMENT, R.A., 1969. Ammonite biostratigraphy, continental drift and oscillatory transgressions. *Nature*, **224**: 137-140.
- RICHARD, D. & M. GUÉDES, 1983. The Papilionidae: coevolution with the angiosperms. *Phyton (Austria)*, **23**: 117-126.
- RILEY, C.V., 1880. Philosophy of the pupation of butterflies, and particularly of the Nymphalidae. *Amer. Ent.*, **3**: 162-167.
- ROBBINS, R.K., 1988. Comparative morphology of the butterfly foreleg coxa and trochanter and its systematic implications. *Proc. ent. Soc. Washington*, **90**: 133-154.
- ROBINSON, R., 1971. *Lepidoptera Genetics*. Pergamon Press, Oxford.
- ROEPKE, W., 1938. *Psychidarbela kalshoveni* n.g., n.sp. (Lep., Cossidae). *Ent. Meded. Ned. Ind.*, **4** (1-2): 22-26.
- ROSEN, D.E., 1974. Cladism or gradism?: a reply to Ernst MAYR. *Syst. Zool.*, **23**: 446-451.
- ROSS, G.N., 1966. Life-history studies on Mexican butterflies. IV. The ecology and ethology of *Anatole rossi*, a myrmecophilous metalmark. *Ann. ent. Soc. Amer.*, **59**: 985-1004.
- ROURKE, M.D., 1986. A preliminary cladistic analysis of the Balfourianae pines based strictly on published character data. *Univ. California, White Mountain Res. Station Symp.*, **1**: 77-83.
- SAETHER, O.A., 1986. The myth of objectivity—post-Hennigian deviations. *Cladistics*, **2**: 1-13.
- SAKURAI, A. & Y. OKUMURA, 1971. Chemical studies on the mistletoe. I. The constituents of *Viscum album* LINN. var. *coloratum* OHWI epiphyting to *Celtis sinensis* PERS. var. *japonica* NAKAI. *Rep. Fac. Sci., Shizuoka Univ.*, **6**: 63-69.
- SAMYLINA, V.A., 1968. Early Cretaceous angiosperms of the Soviet Union based on leaf and fruit remains. *Bot. J. Linn. Soc.*, **61**: 207-218.
- SASTRI, R.L.N., 1969. Comparative morphology and phylogeny of the Ranales. *Biol. Rev.*, **44**: 291-319.
- SCHAEFFER, B., HECHT, M.K. & N. ELDREDGE, 1972. Phylogeny and paleontology. *Evol. Theory*, **6**: 31-46.
- SCHREITER, R., 1943. Notas entomo-biologicas y otras, *Acta Zool. Lilloana*, **1**: 7-44.
- SCOTT, J.A., 1984. The phylogeny of butterflies (Papilionoidea and Hesperioidea). *J. Res. Lep.*, **23**: 241-281.
- 1986a. *The Butterflies of North America*. Stanford University Press, Stanford.
- 1986b. On the monophyly of the Macrolepidoptera, including a reassessment of their relationships to Cossioidea and Castnioidea, and a reassessment of Mimallonidae to Pyraloidea. *J. Res. Lep.*, **25**: 30-38.
- SCUDDER, S.H., 1889a. *The Butterflies of the Eastern United States and Canada, with Special Reference to New England*. W.H. Wheeler, Cambridge, Mass.
- 1889b. The fossil butterflies of Florissant. *8th Ann. Rep., U. S. geol. Survey*, part 1: 433-474, 2 pls.
- SELLIER, R., 1974. Donnees documentaires sur l'ultrastructure des recepteurs sensoriels antennaires chez les Lepidopteres Rhopaloceres: etude en microscopie electronique par balayage. *Ann. Soc. Ent. France (n.s.)*, **10**: 917-937.
- SHAPIRO, A.M., 1979. The life histories of the *antodice* and *sterodice* species-groups of *Tatochila* (Pieridae). *J. New York ent. Soc.*, **87**: 236-255.
- SHAROV, V.A.G., 1965. Evolution and taxonomy. *Zeit. Zool. Syst. Evol.*, **3**: 349-358.
- SHIELDS, O., 1967. Hilltopping. *J. Res. Lep.*, **6**: 69-178.
- 1976. Fossil butterflies and the evolution of Lepidoptera. *J. Res. Lep.*, **15**: 132-143.
- 1977. A Gondwanaland reconstruction for the Indian Ocean. *J. Geol.*, **85**: 236-242.
- 1979. Evidence for initial opening of the Pacific Ocean in the Jurassic. *Palaeogeogr., Palaeoclimat., Palaeoecol.*, **26**: 181-220.
- 1985a. Zoogeography of the Libytheidae (snouts or beaks). *Tokurana (Acta Rhop.)*, **9**: 1-58.
- 1985b. Southeast Asian affinities in Colorado Oligocene Libytheidae. *Tokurana (Acta Rhop. Spec.)*, **1**: 13-24.

- 1987. Presence of pterin pigments in wings of Libytheidae butterflies. *J. chem. Ecol.*, **13**: 1843 – 1847.
- 1988. Mesozoic history and neontology of Lepidoptera in relation to Trichoptera, Mecoptera, and angiosperms. *J. Paleont.*, **62**: 251 – 258.
- & S.K. DVORAK, 1979. Butterfly distribution and continental drift between the Americas, the Caribbean and Africa. *J. nat. Hist.*, **13**: 221 – 250.
- SIBATANI, A., 1973. Taxonomic significance of reflective patterns in the compound eye of live butterflies: a synthesis of observations made on species from Japan, Taiwan, Papua New Guinea and Australia. *J. Lep. Soc.*, **27**: 161 – 175.
- SOBER, E., 1986. Parsimony and character weighting. *Cladistics*, **2**(1): 28 – 42.
- STANLEY, S.M., 1973. An explanation for Cope's Rule. *Evolution*, **27**: 1 – 26.
- 1975. A theory of evolution above the species level. *Proc. nat. Acad. Sci. U. S. A.*, **72**: 646 – 650.
- STEKOL'NIKOV, A.A., 1967. Phylogenetic relationships within the Rhopalocera on the basis of the functional morphology of the genital apparatus. *Ent. Rev.*, **46**(1): 1 – 11.
- STEMPFER, H., 1967. The genera of the African Lycaenidae. *Bull. Br. Mus. nat. Hist., Ent. Suppl.*, **10**: 1 – 322, 1 pl.
- STEVENS, P.F., 1980. Evolutionary polarity of character states. *Ann. Rev. Ecol. Syst.*, **11**: 333 – 358.
- STICHEL, H., 1930. Riodinidae: Nemeobiinae et Riodininae I. *Lep. Catalogus*, **38**: 1 – 112; **40**: 113 – 544.
- STRAND, E., 1909. *Pemphigostola synomonistis* STRAND n.g., n.sp. *Deutsche Ent. Zeit. (Berlin)*, **1909**: 663 – 667.
- 1930. Castniidae. In A. Seitz (ed.), *The Macrolepidoptera of the World*, vol. 14. *The African Bombyces and Sphinges*: 15 – 18. A. Kernen, Stuttgart.
- SWAMY, G.L., 1953. The morphology and relationships of the Chloranthaceae. *J. Arnold Arboretum, Harvard Univ.*, **34**: 375 – 408.
- SWIHART, S.L., 1967. Hearing in butterflies (Nymphalidae: *Heliconius*, *Ageronia*). *J. Ins. Physiol.*, **13**: 469 – 476.
- SZALAY, F.S., 1977. Ancestors, descendents, sister groups and testing of phylogenetic hypotheses. *Syst. Zool.*, **26**: 12 – 18.
- 1981. Functional analysis and the practice of the phylogenetic method as reflected by some mammalian studies. *Amer. Zool.*, **21**: 37 – 45.
- 1982. A new appraisal of marsupial phylogeny and classification. In M. ARCHER (ed.), *Carnivorous Marsupials*, vol.2: 621 – 640. Royal Zoological Society of New South Wales, Mosman.
- TALBOT, G., 1932. Pieridae I. *Lep. Catalogus*, **53**: 1 – 320.
- 1939. *The Fauna of British India, Including Ceylon and Burma: Butterflies*, vol. 1. Taylor & Francis, London.
- THORNE, R.F., 1973. The "Amentiferae" or Hamamelidae as an artificial group: a summary statement. *Brittonia*, **25**: 395 – 405.
- TILLYARD, R.J., 1918. The panorpoid complex. Part 1. The wing-coupling apparatus, with special reference to the Lepidoptera. *Proc. Linn. Soc. New South Wales*, **43**: 286 – 319.
- 1919. The panorpoid complex. Part 3. The wing venation. *Proc. Linn. Soc. New South Wales*, **44**: 533 – 718.
- TINDALE, N.B., 1980. Origin of the Lepidoptera, with description of a new Mid-Triassic species and notes on the origin of the butterfly stem. *J. Lep. Soc.*, **34**: 263 – 285.
- TRIMEN, R., 1887. *South African Butterflies: a Monograph of the Extra-Tropical Species. Vol. 2, Erycinidae and Lycaenidae*. Trubner & Co., London.
- TURNER, A.J., 1918. Observations on the lepidopterous family Cossidae and on the classification of the Lepidoptera. *Trans. ent. Soc. Lond.*, **1918**: 155 – 190.
- 1947. A review of the phylogeny and classification of the Lepidoptera. *Proc. Linn. Soc. New South Wales*, **71**: 303 – 338.

- TUTT, J.W., 1899. *A Natural History of the British Lepidoptera*, vol. 1. S. Sonnenschein & Co., London.
- VAN VALEN, L., 1978. Why not be a cladist. *Evol. Theory*, **3**: 285 – 299.
- VOSS, E.G., 1952. On the classification of the HesperIIDae. *Ann. ent. Soc. Amer.*, **45**: 246 – 258.
- VRBA, E.S., 1980. Evolution, species and fossils: how does life evolve? *South African J. Sci.*, **76**: 61 – 84.
- WAGNER, W.H., Jr., 1980. Origin and philosophy of the groundplan-divergence method of cladistics. *Sys. Bot.*, **5**: 173 – 193.
- WALKER, J.W., 1976a. Comparative pollen morphology and phylogeny of the Ranalean complex. In C.B. BECK (ed.), *Origin and Early Evolution of Angiosperms*: 241 – 299. Columbia University Press, New York and London.
- 1976b. Evolutionary significance of the exine in the pollen of primitive angiosperms. *Linn. Soc. Symp. Ser.*, **1**: 251–292.
- & A.G. WALKER, 1984. Ultrastructure of Lower Cretaceous angiosperm pollen and the origin and early evolution of flowering plants. *Ann. Missouri Bot. Garden*, **71**: 464 – 521.
- WATERHOUSE, G.A. & G. LYELL, 1914. *The Butterflies of Australia*. Angus & Robertson, Sydney.
- WATROUS, L.E. & Q.D. WHEELER, 1981. The out-group comparison method of character analysis. *Syst. Zool.*, **30**: 1 – 11.
- WATSON, J., 1899. On *Calinaga*, the single genus of an aberrant subfamily of butterflies. *Manchester Literary and Philosophi. Soc., Mem. Proc.*, **43**(11): 1 – 23, 3 pls.
- WELLING, E.C., 1958. Some notes on the “excelsior” complex, regarding microtopology with *Heterocera* in Ohio. *Lep. News*, **12**: 131 – 132.
- WHALLEY, P., 1986. A review of the current fossil evidence of Lepidoptera in the Mesozoic. *Biol. J. Linn. Soc. Lond.*, **28**: 253 – 271.
- WHEELER, Q.D., 1986. Character weighting and cladistic analysis. *Syst. Zool.*, **35**: 102 – 109.
- WHIFFIN, T. & M.W. BIERNER, 1972. A quick method for computing Wagner trees. *Taxon*, **21**: 83 – 90.
- WHITE, F.B., 1878. On the male genital armature in the European Rhopalocera. *Trans. Linn. Soc. Lond., Ser. 2 – Zoology*, **1**: 357 – 369, 3 pls.
- WILEY, E.O., 1979. An annotated Linnean heirarchy, with comments on natural taxa and competing systems. *Syst. Zool.*, **28**: 308 – 337.
- 1981. *Phylogenetics: the Theory and Practice of Phylogenetic Systematics*. J. Wiley & Sons, New York.
- WILSON, E.O., 1987. The earliest known ants: an analysis of the Cretaceous species and an inference concerning their social organization. *Paleobiology*, **13**: 44 – 53.
- WITTHOLN, K. & C.M. NAUMANN, 1987. Cyanogenesis — a general phenomenon in the Lepidoptera? *J. chem. Ecol.*, **13**: 1789 – 1809.
- WYNTER-BLYTH, M.A., 1957. *Butterflies of the Indian Region*. Bombay nat. Hist. Soc., Bombay.
- YAGI, N. & N. KOYAMA, 1963. *The Compound Eye of Lepidoptera: Approach from Organic Evolution*. Shinkyō Press, Tokyo.

摘 要

テングチョウ科の分類学的位置, チョウの複
系統性, チョウのガ的祖先 (鱗翅目) (Oakley SHIELDS)

成虫と幼虫の複合的な形態形質 (complex morphological characters) を用いてテングチョウ科の分類学的位置を再評価したところ、テングチョウ科はシロチョウ亜科的祖先から進化し、狭義のタテハチョウ亜科がそこから生じたということが示された。複合的な形態形質とは、羊膜を持つ卵、脊椎動物の目、哺乳類の耳骨などのように、機能的に高度に統合され、直接的な淘汰により共進化するもので、多くの単純な形態形質から構成されている (HECHT, 1976; HECHT & EDWARDS, 1976a, b; STEVENS, 1980)。表 2 や本文中のテングチョウ科のために選ばれた複合的な形態形質の各々は、機能的なユニットであり、さらに 2 つないし多くの単純な形質へ分割されうる。

何人かの研究者はテングチョウの卵と *Mylothris* のようなシロチョウの卵との密接な類似性を指摘してきた (BELL, 1910; WYNTER-BLYTH, 1957; CLARK & DICKSON, 1964; CORBET & PENDLEBURY, 1978)。アメリカテングチョウ *Libytheana backmanni* の幼虫は全体的にタテハチョウ科ではなく、シロチョウ科の幼虫に似ている (PETERSON, 1962 を参照)。頭部は小さく、2 次刺毛でおおわれており、各腹節は 4 ~ 5 の小環に分割されている。タテハチョウ科の幼虫の頭部と体部 (body) または、頭部もしくは体部に存在する体壁の有刺突起 (scoli) を本種アメリカテングチョウは欠く。テングチョウ *L. celtis* の幼虫は、多くの 2 次刺毛を持つ丸く細長いからだ、また頭部の 2 次刺毛により、シロチョウ科の幼虫に似ている。そしてシロチョウ科の幼虫からは pseudocircle の側方にある痕跡的な鈎爪の存在のみにより区別される (FRACKER, 1915)。

テングチョウ科へと進化する潜在的なシロチョウの祖先は、幼虫の食草としてヤドリギを利用している；南米の *Melete* 属は *Phoradendron* (ヤドリギ科) を食し、*Mylothris* 属は *Loranthus* 属とヤドリギ属 (ヤドリギ科)、及び *Osyris* 属 (Santalaceae) を食する。形態的にも *Melete* 属と *Mylothris* 属は密接に関連している (KLOTS, 1931)。 *Melete* 属 (13 種) は熱帯メキシコ、中央アメリカ、南米、キューバ、ヒスパニオラに分布し、他方 *Mylothris* 属 (43 種) はエチオピア区とマダガスカル区に限られている (TALBOT, 1932)。おそらく最初のテングチョウは、幼虫の食草としてヤドリギからエノキ属 (ニレ科) にぎりかえた *Melete* 属または *Mylothris* 属のようなシロチョウから進化したのであろう；例えば日本ではヤドリギはエノキに寄生している (SAKURAI & OKUMURA, 1971)。

アメリカテングチョウはプリテン色素、キサントプリテン、イソキサントプリテン、エリトロプロテン、及びリュウコプリテンを含む。これらの色素のいくつかは、旧世界の数種では欠けているけれども、他のテングチョウ科の種には存在している (SHIELDS, 1987)。シロチョウ科はテングチョウ科を除くとチョウのなかでも、これらの色素を全て有している唯一の科である。プリテンはドクチョウ属 (エリトロプロテン) のある種の翅にもあることが知られており、またタテハチョウ科、シジミチョウ科、シジミタテハ科、そしてアゲハチョウ科 (イソキサントプリテン) の数種にも存在するが、シロチョウ科とテングチョウ科に存在するような配列形は決してとらない。

テングチョウ科はシロチョウ—タテハチョウの特徴を兼ね備えており、一つの独立した科としてみなされる。この結果は分岐学により得られた結果 (編集部注) とはいくぶん異なっているが、分岐学はテングチョウ科のシロチョウ亜科的起源をみのがしてきた。

祖先の幹群法 (symplesiomorphies)、つまり祖先を決定する際に、共有されている原始的な (一般的) 形質を強調する方法、と分岐学的な子孫—分岐法 (synapomorphies) とを組み合わせることは、全体的かつ系統と一致した分類を生み出すに違いない (SZALAY, 1977 を参照)。

BROWN & HEINEMAN (1972) は、テングチョウ科の卵は形の上でシロチョウ科とタテハチョウ科の中間であり、両科でしばしば起こるように、うね状の突起が垂直的に走ると結論づけている。

アメリカテングチョウ属の蛹は尾鉤によりつり下げられており、シロチョウ科とは異なりタテハチョウ科のように糸環を欠いている (EDWARDS, 1884; SCHREITER, 1943; COMSTOCK & GARCIA, 1960). *Libythea laius* の蛹の尾鉤の鉤爪はタテハチョウ科的でシロチョウ科的なものではない (RILEY, 1880; CLARK & DICKSON, 1964参照).

テングチョウ科の翅脈は、ある種のシロチョウ科とタテハチョウ科に非常によく似ているか、同一のものと言ってもよい (GROTE, 1898; 1900).

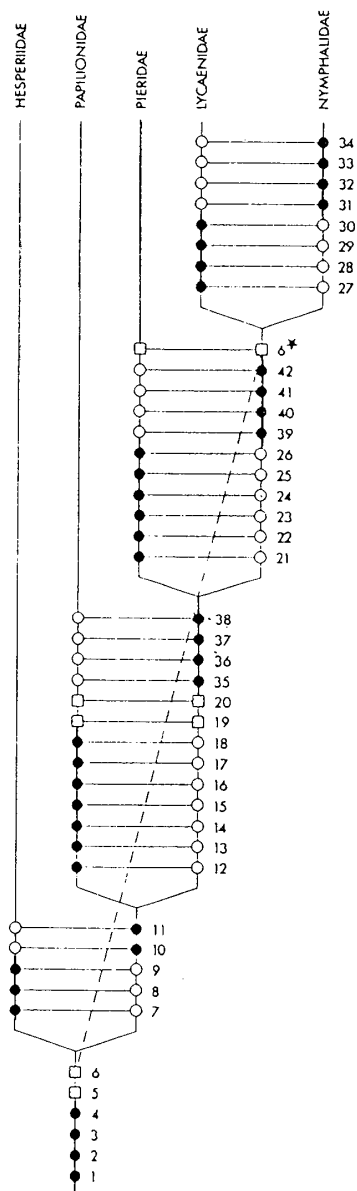
テングチョウ科の前脚の構造 — 雄の前脚は他の脚の 1/4 の長さで、跗節は 1 節、爪または刺を欠く、他方雌の前脚は他の脚よりもやや短い、跗節は 5 節よりなり、爪、副爪、褥盤をもつ — は、タテハチョウ科の雄に似るが、*Pseudogolis* 属を除くすべてのタテハチョウ科の雌とは異なる (JORDAN, 1898). シロチョウ科のように、テングチョウ科の雌の前脚には、2 本の、先端が 2 つにわかれた爪、副爪、褥盤がある (HOLLAND, 1955; EHRLICH & EHRLICH, 1961; COMMON & WATERHOUSE, 1972; HIGGINS, 1975; DICKSON & KROON, 1978; CORBET & PENDLEBURY, 1978; SCOTT, 1986a).

テングチョウ *L. celtis* の雄交尾器の主要な形質は、結局のところこの種をシロチョウ科とタテハチョウ科双方に関連したところへ配列する (WHITE, 1878). テングチョウ属とアメリカテングチョウ属 (SHIELDS, 1985a) の交尾器図をシロチョウ科の属、*Melete* 属と *Mylothris* 属、及び *Euchloina* 族のみと比べてみると、valve, aedeagus, そして uncus-tegumen-vinculum-saccus のあらゆる面で類似している (しかし同一ではない). アメリカテングチョウ属の tegumen の腕状突起は、広くタテハチョウ科に見られる appendix angularis と相同のものである (KAWAZOE & WAKABAYASHI, 1976). テングチョウ属は長い aedeagus の存在、saccus の形状、伸びた突起と鉤爪をもつ valve が存在することで、タテハチョウ科に似ている (SCUDDER, 1889a; MEHTA, 1933). テングチョウ属の valve と、よく発達したキチン質の uncus は、タテハチョウ科のそれらと密接に比較される (FRUHSTORFER, 1914).

伝統的にタテハチョウのなかま翅脈が一致するテングチョウのなかまは、全ての種にみられる長く前方に伸びた吻状の下唇鬚と雌の前脚により区別されてきた (COMMON & WATERHOUSE, 1972). テングチョウ科と比較しうる外観と形をもつ下唇鬚は、*Cyblisia*, *Libythina*, アカタテハ属、そしてソトグロカバタテハ属にみられる (JORDAN, 1925). 現在のシロチョウ科でテングチョウ科と同じくらい長い下唇鬚をもつ種はいないが、*Melete* 属の下唇鬚は 3 節が細く、テングチョウ属のように 2 節よりもはるかに長い (KLOTS, 1931). 漸新世前期のフロリサントから産出したシロチョウ亜科 (シロチョウ族) の化石、*Stolopsyche libytheoides* は長い下唇鬚を有する (SCUDDER, 1889b).

シロチョウ科からシジミチョウ科、ドクガ科までの進化系列をさか上ることができる. チョウ類は多分ヤガ上科から複系統的 (diphyletically) に生じたのである. すなわちドクガ科 — Lipteninae (アフリカ) とトラガ科 — トゲバセセリ亜科 (オーストラリア) という 2 つの系統である.

二門亜目の全体的な発展もまた調べられた. 旧形質共有 (symplesiomorphy) による、非分岐学的群形成法により同定された幹属 (stem genera) (祖先から直接的に由来する属) は、*Psychidarbela* (ボクトウガ科 — ジャワ), *Pemphigostola* (トラガ科 — マダガスカル), *Ancarista* (トラガ科 — マダガスカル), *Apoprogon* (Apoprogonidae, シャクガ上科 — 南アフリカ), *Euschemon* (トゲバセセリ属 — オーストラリア), *Lamproptera* (ソビキアゲハ属 — 東南アジア), そして *Libytheana* (アメリカテングチョウ属 — 北米) である. これらの幹属から種々の二門亜目の科が由来した. その結果生じたチョウ類各科の進化はコープの法則に従う. プレートテクトニクス概念から引き出される推測と、鱗翅類ではないがそれらに関連した化石は、トラガ科は mid-Oxfordian, トゲバセセリ亜科は Albian, シジミチョウ科は Cenomanian が、それぞれの戦略的起源時 (strategic origin times) であることを示している. (文責 編集部)



編集部注. 分岐学的手法により得られたチョウ類各科の分岐図の一例 (KRISTENSEN, 1976).
 数字は用いられた形質の番号. ●…新形質, ○…旧形質, □…確定的でない形質. 「テングチョウ科」, 「マダラチョウ科」, 「ジャノメチョウ科」, 「モルフォチョウ科」等は「タテハチョウ科」に含まれている.